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GALATHEA REPORT

Volume 1

Scientific Results
of The Danish Deep-Sea Expedition
Round the World 1950-52

ISSUED BY THE GALATHEA COMMITTEE
PRESIDENT: H.R.H. PRINCE AXEL OF DENMARK

EXECUTIVE EDITORS:

Anton F. Bruun, D. Sc., LL. D.
Leader of the Expedition

Sv. Greve, Captain, R. D. N.
Commander of the Galathea

R. Spärck, D. Sc.
Professor of Zoology, Vice-President of the Committee

COPENHAGEN
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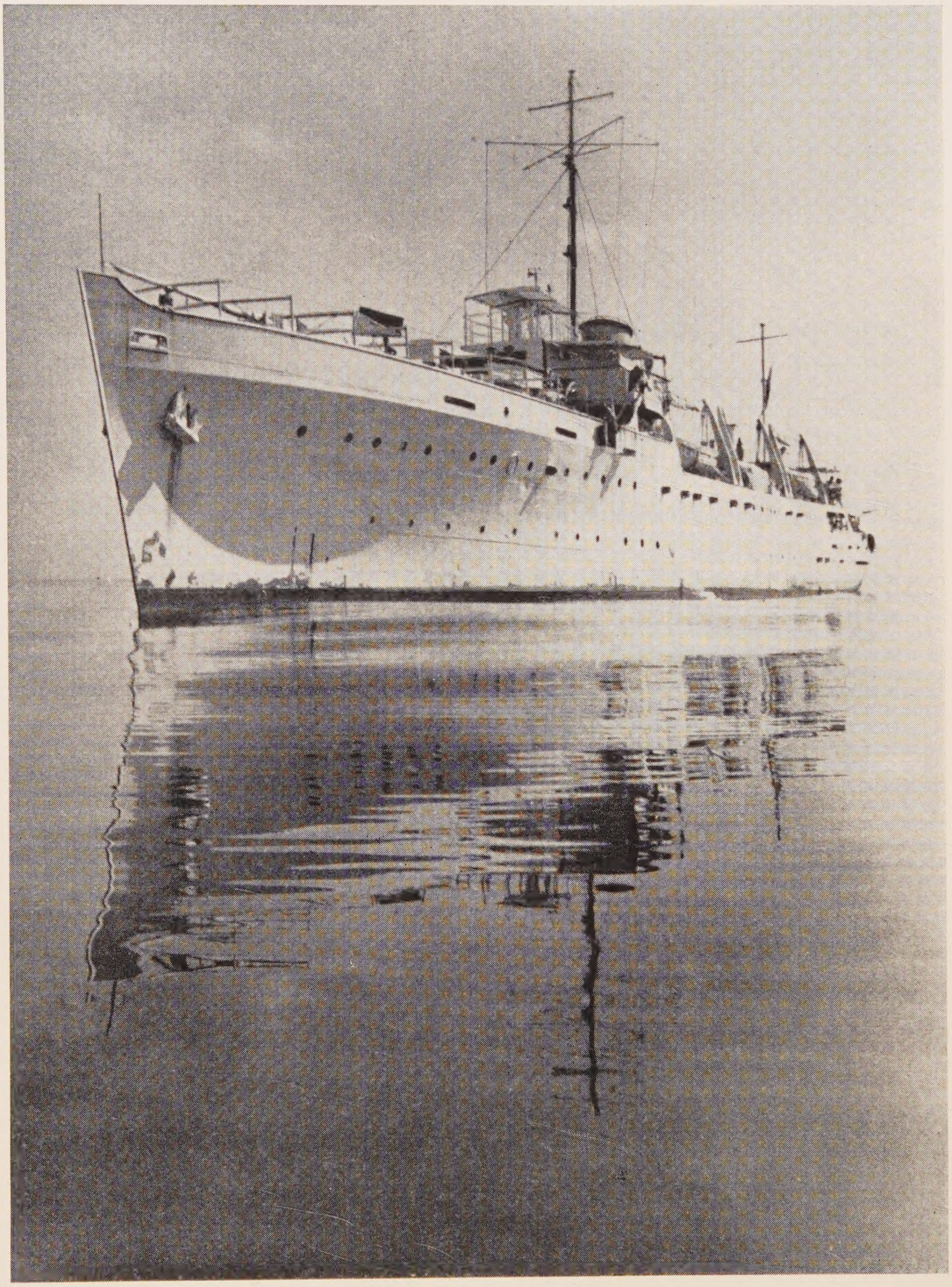

Fig. 1. The Galathea in the Indian Ocean.

GENERAL INTRODUCTION TO THE REPORTS AND LIST OF DEEP-SEA STATIONS

By ANTON F. BRUUN
Zoological Museum, Copenhagen

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1. HISTORY, SHIP, EQUIPMENT AND NARRATIVE

It is not necessary here to give a detailed description of the items of the heading of this chapter; in fact, it would be to duplicate what has been published especially in 1956 in the book: The Galathea Deep Sea Expedition 1950-52, described by Members of the Expedition. This book was a translation of the Danish edition which appeared in 1953 (see BRUUN et al. 1953); this latter book contains a full list of all the persons participating in the preparation and the realization of the expedition. But still earlier a series of more popular books (MIELCHE 1952a, 1952b, 1953) were published in Danish, giving some of the essential scientific achievements, but especially being a narrative of the expedition; these three books have later been united into a one volume edition and translated into several other languages (e.g. MIELCHE 1954).

So in view of this only certain points of importance will be mentioned here, and to facilitate further studies in connection with the expedition a list of references is given at the end of the General Introduction (p. 20) and another list of publications which contains, in whole or in part, results from the expedition, also from the many-sided activity outside the main task, biological deep-sea research (p. 18).

Administration. A special committee under the presidency of H. R. H. Prince AXEL, responsible for the whole expedition was formed in 1948 and so as to cover all aspects in connection with the plans, the economy, and the personel (see p. 10). The expedition was formally a Danish Government expedition, but in reality a joint task of the Royal Danish Navy, the Zoological Museum of the University of Copenhagen, and the Danish Expeditions Fund. This last-named fund, by its president vice-admiral A. H. VEDEL, R. D. N., D. Sc. h. c., and its general secretary Mr. LEIF B. HENDIL, in fact provided the very first grant for the start of the expedition, and by taking over all the expenditure of the scientific equipment made it possible to approach the Danish Government and ask its Royal Navy to furnish a ship and crew for two years. For details see SPÄRCK 1953 and 1956.

The Ship and her Complement. The Galathea was a former naval sloop with a displacement of 1600 tons, built at Devonport in England in 1934. In 1949 she was purchased by the Danish Admiralty with a view to her use on the projected deep-sea expedition. The vessel's length was about 80 m, the width 11 m, and the draught about 3.5 m. The main machinery consisted of two geared high-pressure and low-pressure turbines with a combined horse-power of 2000. On the two oil-fired boilers her maximum speed was 12 knots, and our action range at an economic speed was about 6000 nautical miles. Reconditioning and fitting out as an oceanic research vessel took place at the Royal Naval Dockyards in Copenhagen. A rough lay-out is

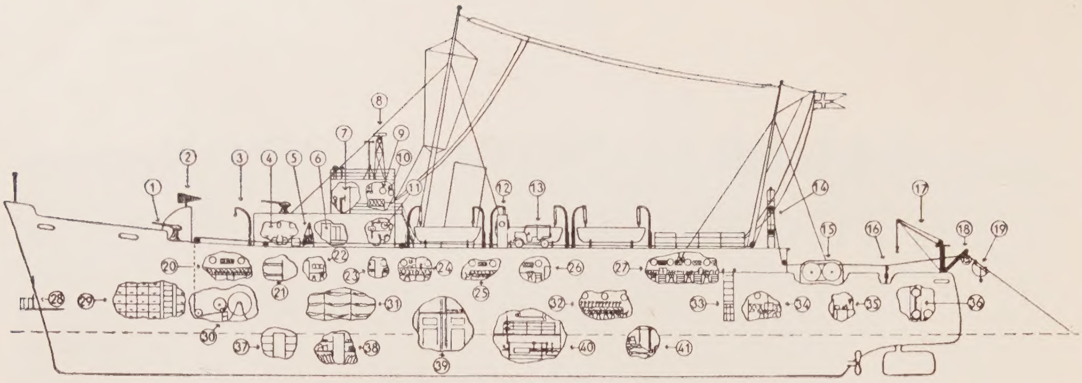

Fig. 2. Lay-out of the Galathea: **1** Salute gun. **2** Fixed insect-catching net. **3** Starbord davit for hauling up bottom samples from shallow water. **4** Reception mess. **5** Hydrography winch on port side. **6** Commander's cabin. **7** Wheel-house. **8** Radar. **9** Chart-house. **10** Echo-sounder. **11** Radio station. **12** Photographic tank for taking under-water films. **13** Jeep. **14** Accumulator for regulating tension of wire between winch and drum. **15** The big trawling winch. **16** Dynamometer for gauging tension of wire. **17** Crane for putting out heavy gear. **18** The big trawl gallows. **19** Angle gauge fixed to wire. **20** Orlop deck. **21** Sick cabin. **22** Consulting cabin. **23** Canteen. **24** Petty Officers' cabin. **25** Petty Officers' mess. **26** Leader's cabin. **27** Laboratory. **28** Removable harpooning platform. **29** Hold for scientific collections. **30** Drum for the large wire, course of the latter over the deck being as shown. **31** Sleeping deck. **32** Officers' and scientists' mess. **33** Removable angling chair. **34** Officers' cabins. **35** Dark-room. **36** Gear hold containing spheres for magnetic surveys. **37** Cold stores. **38** Pantry. **39** Stokehold. **40** Engine-room. **41** Deep-freezing store.

given in fig. 2. The result was a very good sea-boat, steady even in quite rough weather, and with negligible vibrations interferring with microscopic work. For details see GREVE 1953 and 1956. The full complement was a little over a hundred. Complete lists of names are given by BRUUN et al. 1953, pp. 297 to 300. On pp. 10-11 are given lists of all the personel who took a direct part in the special activity of the ship, the responsible navigators, scientists and technicians. A special feature of the ship was the ever changing complement except for about half of it serving the whole expedition. This was a happy combination of keeping a continuity of experience with refreshing additions of specialists for longer or shorter periods of time. Seven foreign scientists were invited to cover special fields and 29 others were invited onboard from the countries along the route. The success of this feature has been described by WOLFF (1953, 1956).

Objects of the Expedition. – These have been

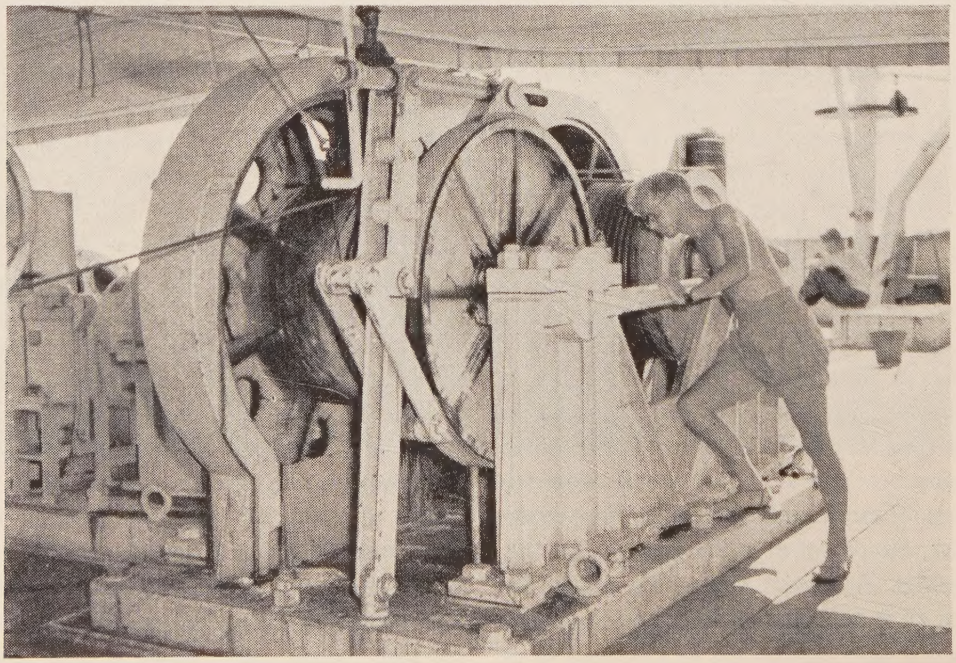

Fig. 3. Part of the electrical winch on the aft deck.

summarized by BRUUN (1953, 1956), and it is hoped that the titles of the publications listed in this paper and the scientific reports of which this is the introduction will sufficiently show that an essential part of the programme was carried out as planned.

The Technique of Deep-Sea Trawling. The Expedition had a very great advantage in being able to utilize the new technique used so successfully by the Swedish Deep-Sea Expedition 1947-1948 (NYBELIN 1951), even to the extent that the Galathea acquired three winches from this expedition (fig. 3), and still more important, could profit from the personal experience of Prof. O. NYBELIN and Prof. B. KULLENBERG both before the Galathea started and when they accepted the invitation to come onboard for some time. KULLENBERG (1953, 1956) has described the special features of the technique as adapted to the conditions on the Galathea. A full description of the winches has been given by KULLENBERG and MICHAELSON (1954) and JERLOV, KOCZY, KULLENBERG and MICHAELSON (1957), while KULLENBERG (1951) contains the method of calculating the correct length of the cable for towing trawls or dredges along the deep-sea bottom.

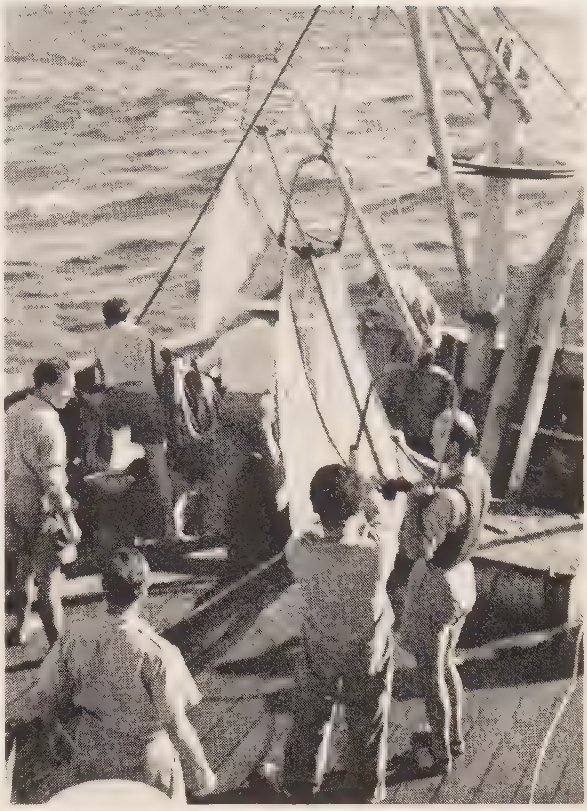
Fig. 4. The 6 m sledge trawl being put out.

Acknowledgments. An innumerable number of persons, in Denmark and all over the world, gave, in some way or other, support and advice or took an active part in the tasks of the expedition, from the time when Captain Greve many years ago listened to the author's first vague outlines of a deep-sea expedition till the return of the Galathea. Without this grand collaboration the expedition would never have become a reality, so the author would like to end this chapter by expressing his deep gratitude to every single person adding to the fulfilment of his youthful dreams.

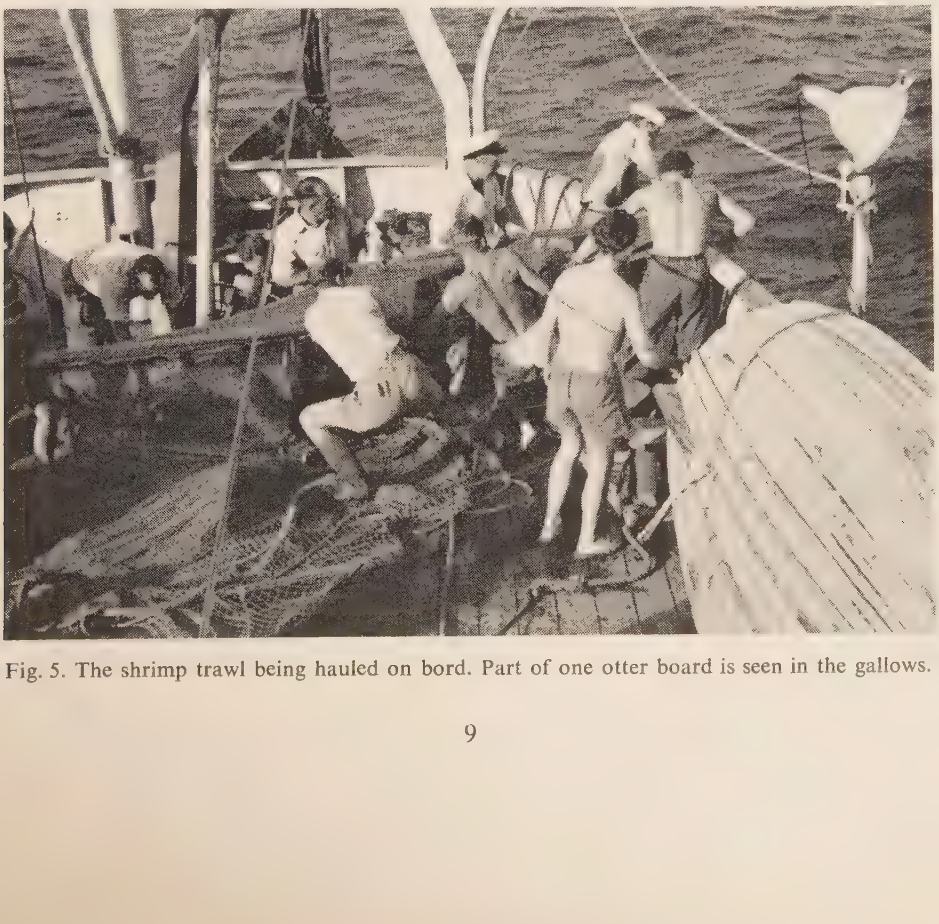
Fig. 5. The shrimp trawl being hauled on bord. Part of one otter board is seen in the gallows.

2. THE COMMITTEE OF THE EXPEDITION

The Executive Committee:

H.R.H. Prince Axel, President
Professor August Krogh, Vice-President, died 1949
Professor R. Spärck, Vice-President from 1949
Professor Niels Bohr
Dr. A.F. Bruun, Scientific Leader of the Expedition
Captain S. Greve, R.D.N., Commander of the Galathea
Mr. C.C.F. Langseth, Ministry of Defence
Mr. E. Lindgren, Ministry of Defence
Mr. Hakon Mielche, Public Relation Officer of the Expedition
Vice-Admiral A. H. Vedel, R.D.N., D.Sc.h.c.

Mr. Verner Christiansen, Secretary of the Committee.

Consultative Members:

Dr. N. Arley, Physics
Dr. K. Birket-Smith, Ethnology
Dr. H. Blegvad, Director Danish Biological Station, died 1951
Mr. C. A. C. Brun, Ministry of Foreign Affairs
Dr. M. Degerbøl, Zoology
Mr. P. Jensen, Hydrographic Office
Professor Martin Knudsen, Hydrography, died 1949
Dr. P. L. Kramp, Zoology
Dr. Th. Mortensen, Zoology, died 1952
Mr. K. Paludan-Müller, Ministry of Education
Mr. H. Petersen, Director Meteorological Institute
Professor E. Steemann Nielsen, Phytoplankton
Mr. H. Thomsen, Hydrography

3. PARTICIPANTS IN THE EXPEDITION

Danish Scientists:

Name	Field	Service
Andreasen, P., Engineer	Magnetism	6.10.50 – 17.7.52
Arley, N., D.Sc.	Magnetism	6.9.50 – 8.10.50 25.10.50 – 20.12.50
Benzon, B., D.Sc.	Zoology	27.12.51 – 11.1.52
Birket-Smith, K., D.Sc.	Etnology	17.6.51 – 31.10.51
Bruun, A.F., D.Sc.	Zoology	1.9.50 – 17.7.52
Degerbøl, M., D.Sc.	Zoology	27.12.51 – 29.1.52
Egedal, J., Ph.D.	Magnetism	6.9.50 – 16.9.50 13.10.50 – 16.12.50
Espersen, J., Ph.D.	Magnetism	4.2.52 – 17.7.52
Hansen, B., Ph.D.	Zoology	1.9.50 – 17.7.52
Jensen, E. Aabye, M.Sc.E.	Chemistry	1.2.52 – 17.7.52
Kiilerich, A., Ph.D.	Hydrography	2.6.51 – 29.9.51
Kirkegaard, J., Ph.D.	Zoology	15.12.50 – 22.3.51
Kramp, P.L., D.Sc.	Zoology	19.3.51 – 29.9.51
Lemche, H., D.Sc.	Zoology	1.12.51 – 17.7.52
Madsen, F. Jensenius, Ph.D.	Zoology	22.6.51 – 17.7.52
Nielsen, E. Steemann, D.Sc.	Phytoplankton	25.10.50 – 19.1.51
Olsen, J., Ph.D.	Magnetism	6.9.50 – 16.9.50 13.10.50 – 16.3.51
Pfaff, J. R., Ph.D.	Zoology	15.12.50 – 26.5.51
Spärck, R., D.Sc.	Zoology	6.10.50 – 8.10.50 15.12.50 – 6.1.51 19.3.51 – 22.3.51
Vilstrup, T., M.D., D.Sc.	Zoology	2.2.52 – 16.4.52
Volsøe, H., D.Sc.	Zoology	19.3.51 – 26.5.51
Wolff, T., Ph.D.	Zoology	1.9.50 – 17.7.52

Foreign Scientists

Name	Field	Service
Bolin, R.L., D.Sc., USA	Zoology	8.1.52 – 11.4.52
Gislén, T., D.Sc., Sweden	Zoology	22.6.51 – 10.11.51
Kullenberg, B., D.Sc., Sweden	Oceanography	6.9.50 – 16.9.50 6.10.50 – 8.10.50 15.12.50 – 12.2.51
Morita, R.Y., M.Sc., USA	Microbiology	9.2.52 – 12.4.52
Nybelin, O., D.Sc., Sweden	Zoology	6.9.50 – 16.9.50
Pickford, Grace, D.Sc., USA	Zoology	16.4.51 – 9.7.51
ZoBell, C.E., D.Sc., USA	Microbiology	9.7.51 – 2.10.51

Public Relation Service

Benzon, J.	Journalist	13.10.50 – 5.6.51
Høyer, M.	Photographer	22.6.51 – 17.7.52
Mielche, H.	Head P.R.S.	1.9.50 – 20.3.51 17.6.51 – 1.11.51 2.1.52 – 17.7.52
Nielsen, J.	Photographer	13.10.50 – 19.1.51
Rasmussen, P.	Photographer	1.9.50 – 17.7.52

Officers of the Royal Danish Navy

Barfoed, S.H.L., Commander	Executive officer	15.1.51 – 17.7.52
Christensen, J., Ltnt.-comdr.	Officer of the watch	4.9.50 – 17.7.52
Crilsen, C., Ltnt.-comdr.	Engineer	11.2.51 – 17.7.52
Feddersen, T.G., Commander	Medical officer	1.9.50 – 29.9.51
Ferdinand, L., Ltnt.	Medical officer	15.9.51 – 17.7.52
Flemming, V.C.A., Count of Rosenborg, Ltnt.-comdr.	Officer of the watch	1.9.50 – 12.6.51
Greve, S.B.V.J., Commodore	Commanding officer	13.2.51 – 17.7.52
Hansen, N.E., Ltnt.	Engineer	1.9.50 – 17.7.52
Koch Jensen, G.A., Commander	Chief-engineer	1.9.50 – 21.11.51
Lessél, O., Captain	Chief-engineer	15.12.50 – 29.6.51
Madsen, C.H.A., Captain	Commanding officer	1.9.50 – 13.2.51
Seehusen, K.H., Captain	Executive officer	1.9.50 – 15.1.51
Thegler-Jensen, A.C., Ltnt.-comdr.	Engineer	1.9.50 – 28.6.51
	Chief-engineer	29.6.51 – 17.7.52
Thorsen, A. W., Ltnt.-comdr.	Officer of the watch	12.6.51 – 17.7.52
Thygesen, N.J., Petty officer	Radio, echo-sounder	1.9.50 – 17.7.52
Westergaard, I., Commander	Navigating officer	1.9.50 – 17.7.52

University Students on National Service in RDN

Crossland, I., B.Sc.	Chemistry	1.9.50 – 17.7.52
Degerbøl, J., LL.B.	Secretary of the Scientific Leader	1.9.50 – 5.6.51
Horsted, Sv.Aa., B.Sc.	Zoology	1.9.50 – 26.5.51
Jacobsen, P. Holmelund, B.Sc.	Zoology	22.6.51 – 17.7.52

Name	Field	Service
Jensen, E. Aabye, M.Sc.E.	Chemistry	1.9.51 – 31.1.52
Jensen, K.E., Ph.D.	Zoology	22.6.51 – 17.7.52
Kläning, U., B.Sc.	Chemistry	1.9.50 – 17.7.52
Knudsen, H., B.Sc.	Zoology	22.6.51 – 17.7.52
Marckmann, K.V., Ph.D.	Zoology	1.9.50 – 26.5.51
Nielsen, J., B.Sc.	Zoology	1.9.50 – 26.5.51

Visiting Scientists

Batham, Elisabeth, Ph.D., New Zealand	Zoology	12.1.52 – 22.1.52
Bennett, Isobel, Australia	Zoology	1.12.51 – 15.12.51
Brodie, F.W., New Zealand	Oceanography	11.1.52 – 22.1.52
Cassie, R.M., M.Sc., New Zealand	Zoology	24.1.52 – 27.1.52
Chavernphol, Swarng, Thailand	Zoology	18.6.51 – 9.7.51
Davies, D., South Africa	Zoology	19.1.51 – 9.2.51
Dell, R.K., M.Sc., New Zealand	Zoology	24.1.52 – 26.2.52
Downie, R., Captain, Australia	Trawling	1.12.51 – 15.12.51
Falla, R., Ph.D., New Zealand	Zoology	27.12.51 – 11.1.52
Fleming, C.A., D.Sc., New Zealand	Marine Geology	11.1.52 – 22.1.52
Hardenberg, J.D.T., D.Sc., Indonesia	Zoology	1.9.51 – 16.9.51
Harry, R.R., Ph.D., USA	Zoology	10.4.52 – 12.4.52
Medina, R., Philippines	Zoology	10.7.51 – 25.7.51
Megia, T., Philippines	Hydrography	10.7.51 – 11.8.51
Moreland, J., M.Sc., New Zealand	Zoology	27.12.51 – 8.1.52
Powell, A.W.B., New Zealand	Zoology	23.1.52 – 26.1.52 12.2.52 – 26.2.52
Prasad, R., Ph.D., India	Zoology	19.4.51 – 12.5.51
Ramage, F., England	Echo-sounding	20.10.50 – 24.10.50
Rayner, G., Australia	Zoology	10.11.51 – 14.11.51
Ronquillo, I., Philippines	Zoology	25.7.51 – 11.8.51
Sidwell, P.M., England	Echo-sounding	20.10.50 – 24.10.50
Sparling, S.C., England	Echo-sounding	20.10.50 – 24.10.50
Turbott, G., Ph.D., New Zealand	Zoology	12.2.52 – 26.2.52
Veen, Ch., Indonesia	Hydrography	1.9.51 – 16.9.51
Whitley, G.P., Australia	Zoology	8.11.51 – 15.12.51
Willimowsky, N.J., Ph.D., USA	Zoology	10.4.52 – 12.4.52
Wood, F., Ph.D., Australia	Microbiology	1.12.51 – 7.12.51
Yapchiongcho, J.N., Philippines	Zoology	27.7.51 – 11.8.51

4. THE ECOLOGICAL ZONATION OF THE DEEP-SEA BOTTOM FAUNA

The activity of the Galathea Expedition was focussed at the bottom fauna of the deeper and deepest parts of the ocean; but a considerable effort was also made in shallower depths. This effort served several purposes; the first one was simply to obtain experience and prove the efficiency of the various gear under less difficult conditions, because in general, the greater the depths the greater become the difficulties of the operations.

Other important aspects were however also kept in mind. For the treatment of the abyssal and hadal faunas it might be very useful to get an idea of the composition of the shallower faunas both in respect to quantity and quality. This should also furnish some background for a study of the vertical distribution of many animals; unfortunately, a great number of deep sea animals are so poorly known and described that the taxonomic situation very often is quite obscured. Therefore, it is to be hoped that the numerous specimens from the Galathea Expedition may clear up many such problems which are more easily solved when for the study of a particular group, a relative abundance of material is available, from many parts of the ocean and at the same time from many different depths.

It goes without saying that spending two years with this kind of work, and with a background of several more years of collecting animals also in coastal regions and the pelagic zones of the deep sea from the arctic to the subantarctic latitudes, gives a certain general picture of the ecological situation of the deep sea.

The Galathea Reports will mainly comprise the animals from the bottom at depths exceeding 400 m.

For the sake of uniformity of ecological terminology in these reports the many collaborators should consult the same standard work in this field: Treatise on Marine Ecology and Paleoecology, vol. 1, Ecology, edited by JOEL W. HEDGPETH, being Memoir 67 of the Geological Society of America, 1957.

When, sometime, the collections from the Galathea Expedition have been worked up, and at the same time many more results have been published from other expeditions, a revision of the general picture of today will most certainly be needed. But for the time being the following considerations are presented in line with the Treatise on Marine Ecology and similar suggestions given elsewhere (e.g. BRUUN 1956).

The 400 m curve was chosen because this depth is well below the photic zone, and, from the geological point of view, outside the continental shelf or some way down the continental slope: the *deep sea,* this very vague term, is about but certainly not the abyss. In some geographical areas this modest depth of 400 m is even not below the thermocline, meaning that temperatures may run above 10°C. In consideration of the importance of the situation of the thermocline so clearly seen in the distribution of the pelagic communities of the open ocean, it seems essential always to study the distribution of benthic faunas in their relation both to temperature and depth.

HEDGPETH (1957, p. 23) is perfectly right in his statement: For some reason ecologists have not as yet paid as much attention to the temperature as a factor in the major divisions of the oceans, although it is of primary concern to biogeography.

But this involves some difficulty as to the terminology if we want to use the parallel terms of the benthic and pelagic communities of greater depths. If, e.g., the term *bathyal* is used in consistency with the term *bathypelagic,* it is implied that the environment is aphotic and below the thermocline in a temperature range between about 4° to 10°C. For the pelagic environment above the thermocline, but in the aphotic zone, the very useful term *mesopelagic* has been adopted (HEDGPETH 1957, p. 18, fig. 1); no corresponding term for the benthic environment seems available. It should in fact cover the lower part of the Outer Sublittoral of HEDGPETH and at the same time express that the temperatures are similar to those of the mesopelagic zone, i.e. above 10°C. To avoid adding to the confusing state of terminology of the shelf environment the coining of such a term should be delayed until many more studies have been made of the importance of the combination of temperature and depth in the distribution of animals in the deeper part of the Outer Sublittoral, especially in relation to the thermocline where this feature is present and most pronounced.

Below the thermocline, or at temperatures below about 10°C. in the regions outside the range of the thermosphere, the bathypelagic zone has its corre-

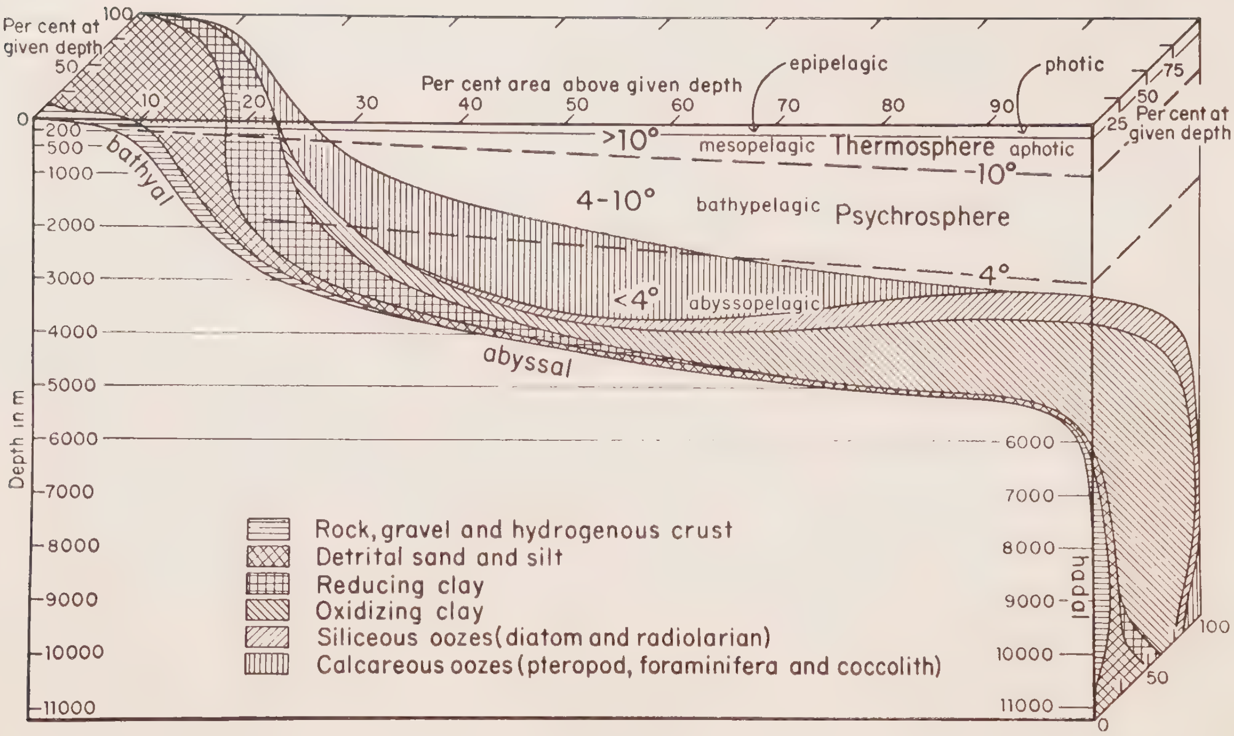
Per cent at given depth
100
50
0
10
20
30
Per cent area above given depth
40
50
60
70
80
90
epipelagic
photic
75
50
25
Per cent at given depth
200
500
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
Depth in m
bathyal
>10°
mesopelagic
Thermosphere
aphotic
-10°
4-10°
bathypelagic
Psychrosphere
4°
<4°
abyssopelagic
abyssal
hadal
100
50
0
Rock, gravel and hydrogenous crust
Detrital sand and silt
Reducing clay
Oxidizing clay
Siliceous oozes (diatom and radiolarian)
Calcareous oozes (pteropod, foraminifera and coccolith)

Fig. 6. Ecological zonation of the deep-sea.

sponding benthic zone, the *bathyal* which extends downwards and polewards until the temperature goes around 4° C.

Correspondingly the abyssopelagic zone of the open ocean has its benthic counterpart in the *abyssal* zone with temperatures below about 4° C, mostly 1° to 2° C.

Finally, the deepest parts of the oceans, the trenches with depths exceeding 6000 m, contain a special benthic assemblage of species forming the *hadal* fauna.

Ever since REGNARD (1891) and later e.g. FONTAINE (1930) and EBBECKE (1935) the hydrostatic pressure has been suggested as an important ecological factor in the deep sea. These experimental physiologists, using shallow-water animals, found a wide range of tolerance towards a high pressure in the various animal groups and even of the different stages of life or different isolated organs of the same species. This was in good agreement with the empirical finding of eurybathic and stenobathic animals. But the final proof came from the catch of species living only in the trenches, and, most important, from the studies of barophilic bacteria from the Philippine Trench (ZOBELL 1952, ZOBELL and MORITA 1959). In view of this it is not so surprising that a species like the holothurian *Elpidia glacialis* quite recently could be considered a characteristic arctic deep-sea species (EKMAN 1953, p. 298) when it should rather be regarded as being typically a cosmopolitan abyssal species of a relatively high quality of eurybathy combined with some eurythermy (HANSEN 1956).

It is only when the geographical distribution of the single species is reasonably well known and has been studied in relation to depth, temperature, oxygen, sediments, food supply and other important ecological factors that a fuller understanding may be reached. In this connection a comparative study of the faunas of bassins isolated from the open ocean by sills at various levels are of particular interest, especially by the North Polar Sea, the Mediterranean Sea, the Red Sea, and the Sulu Sea. Equally important is a comparison of the hadal fauna in its geographical diversity so similar to the terrestrial alpine faunas and floras.

It has long been known that species living in the bathyal and abyssal zone may lead a larval life in quite a different zone. An extreme case are species of the deep-sea eel *Synaphobranchus*, whose larvae live in the epipelagic zone of the tropics and subtropics, while adolescent and adult specimens are even abyssal (BRUUN 1937). In such a case suitable breeding places more than anything else determine the distribution of the species; but also the adolescent and adult stage are naturally limited by their own ecological requirements as when the North Atlantic species *S. kaupi* lives just outside the Strait of Gibraltar, but does not occur in the corresponding depths in the Mediterranean where much higher temperatures prevail.

In view of this example it would be of great interest to study the sexual state of the animals whenever possible. Many cases of eurybathy may naturally be ascribed to the spotwise sounding method used until recent years; this is very clearly borne out by the continuously recording echo-sounding methods used nowadays with any deep-sea trawling or dredging. But the turbidity currents and mudslides may also play some role in carrying animals from the continental slopes into greater depths, as the case may be from the bathyal into the abyssal zone; such animals might very well live and grow in the new environment but remain sterile, and thus give a false impression of the normal distribution of the species.

5. REMNANTS OF PLANTS FOUND IN THE DEEP-SEA

Already at an early stage of deep-sea research remnants of plants from land or the coastal belt have been observed (Agassiz 1888, p. 291). The importance of such organic matter in relation to the food supply in the aphotic zone has been discussed elsewhere (Bruun 1957, pp. 655-661).

During the Galathea expedition any plant débris was preserved for possible later identification. Therefore, it has also been possible to give a rough picture of its quantity and distribution along the route which may be useful for considerations regarding the distribution of various animal groups. Fig. 7 gives a general picture while table 1 contains a certain amount of details. Due to the variety of gear used no true comparative study of the quantities could be made, but figures have been given indicating the amount by volume and weight after drying in the air. Besides, a certain characterization of the kind of material has been attempted.

It is perhaps especially remarkable that some material was recovered from the depths exceeding 7000 m in the trenches, even right down to the bottom of the Philippine Trench. The greatest amount was naturally found in regions not very far from the mouths of big rivers with mangroves or Pandanus swamps. As examples may be mentioned the South East Asian Seas and the Panamanian region.

Apart from the biological significance of the plants as a source of food when turned into bacteria, which may serve as a first link in a secondary food chain, these observations may be of some relevance for the interpretation of cores of deep-sea sediments. A mudslide or turbidity current might easily bury the plant remnants, making them fossils rather surprising in the deep-sea.

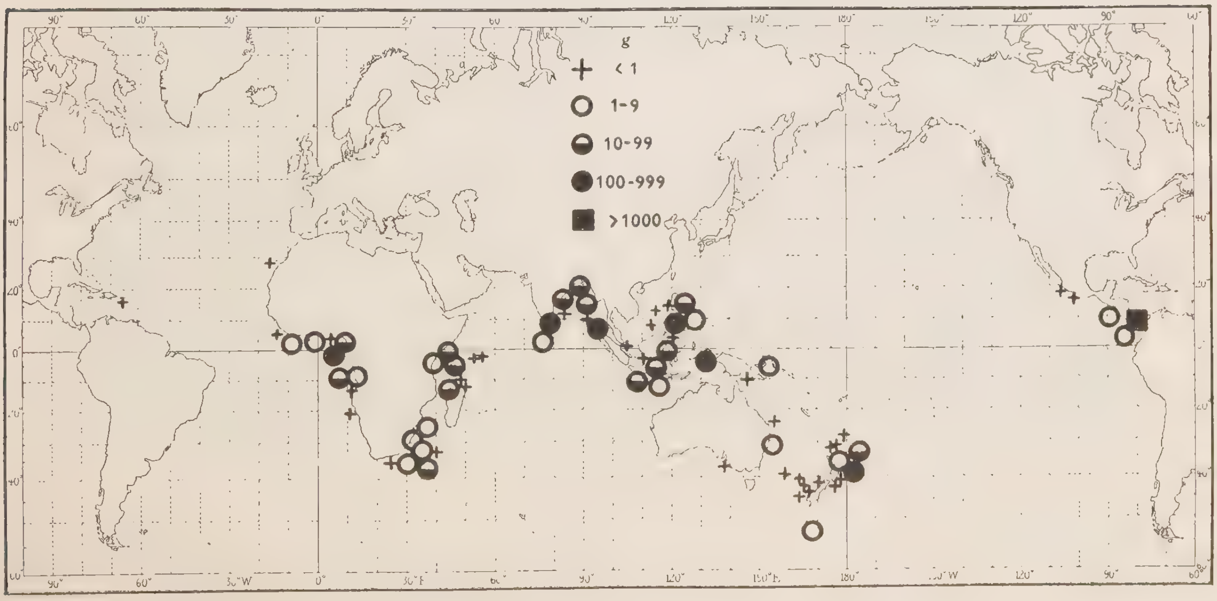

Fig. 7. Remnants of plant material collected along the route of the expedition. Ciphers in g.

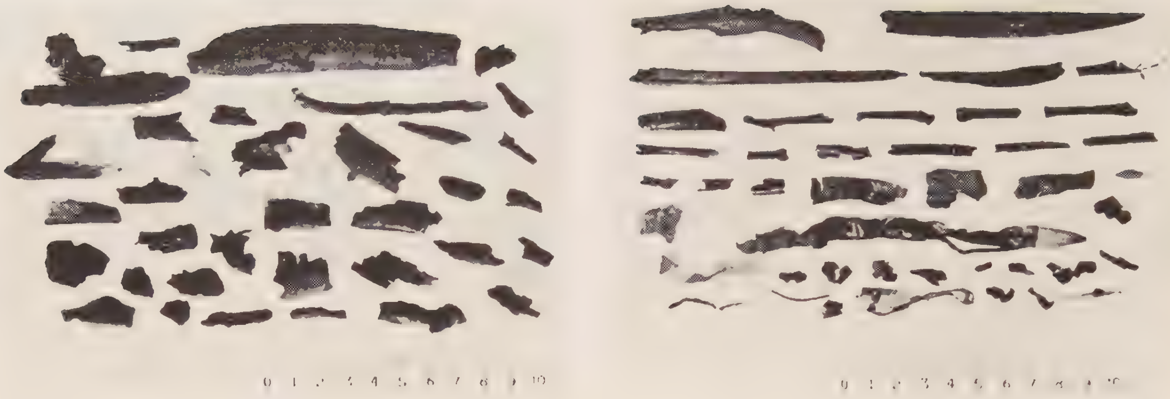
0 1 2 3 4 5 6 7 8 9 10
0 1 2 3 4 5 6 7 8 9 10

Fig. 8. Remnants of plants from the Philippine Trench; left: St. 419 (10.150-10.210 m); right: St. 418 (10.190-10.150 m).

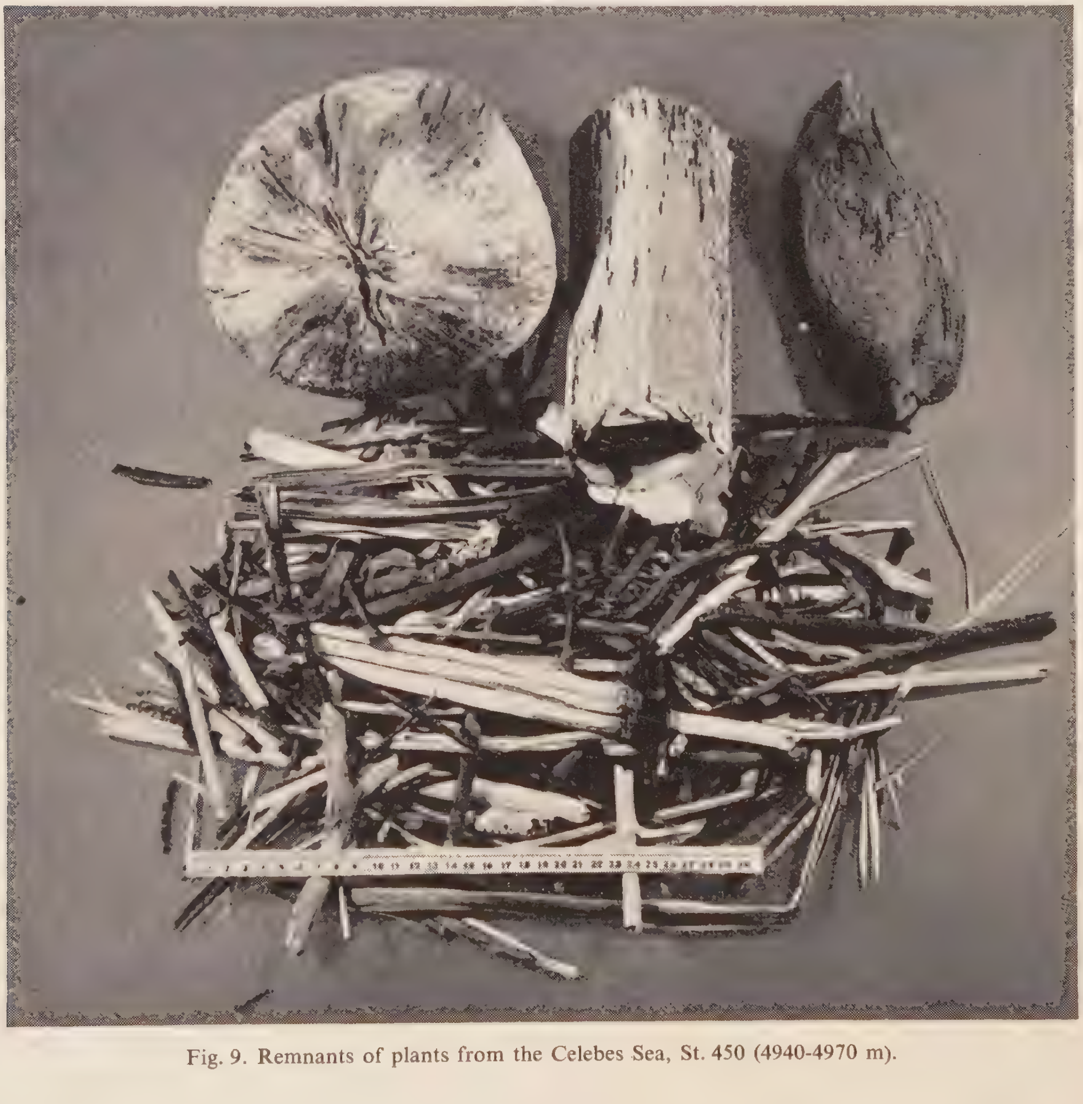

Fig. 9. Remnants of plants from the Celebes Sea, St. 450 (4940-4970 m).

Table 1. Remnants of Plants

St. No.	Depth in meters	Gear (cf. p. 22)	Total		Branches and twigs		Coconut husk		Fruit of Pandanus		Large-sized seeds and shells		Bark		Leaves		Pieces of wood and chips		Various	
			ccm	g	ccm	g	ccm	g	ccm	g	ccm	g	ccm	g	ccm	g	ccm	g		
24	3200	ST 300	2	2	1	1							1	1						
32	2100	SOT	1	1									1	1						
52	2550	SOT	320	275	250	150	55	90							15	35				
63	1520	SOT	35	50	35	50														
99	2690	SOT	22	26	20	25							2	1						
101	990	ST 300	4	3	2	1					1	1	1	1						
180	5220	ST 300	5	10	5	10														
192	3530	SOT	25	35									25	35						
194	4360	SOT	10	5	10	5														
196	430	ST 300	7	5	5	2							1	1			1	2		
202	575	HOT	25	8	25	8														
217	3390	HOT	35	32	10	5							5	2			20	25		
232	4930	HOT	28	12	25	10													3	2
234	4820	HOT	33	14	30	10							1	2					2	2
235	4810	HOT	47	29	30	12					10	12					7	5		
238	3960	HOT	30	15	20	10											10	5		
241	1510	HOT	5	4	3	2											1	1	1	1
279	4320	ST 300	4	2	2	1							2	1						
280	4350	SOT	2	1							2	1								
281	3310	ST 300	5	3	5	3														
282	4040	HOT	690	435	650	400					15	15					25	20		
299	2820	HOT	110	80			100	75									10	5		
302	1190	ST 300	41	21	20	5					10	10	10	5	1	1				
314	2600	HOT	140	80	15	10					25	20					100	50		
324	1140	ST 300	225	125			75	25	75	75							75	25		
418	10150	ST 300	25	20	5	5					15	10	4	4			1	1		
419	10150	ST 300	75	40							40	30	35	10						
429	10020	ST 300	2	12	1	1									1	1				
436	710	ST 300	18	12	2	1									1	1	15	10		
443	1500	ST 300	1105	602	200	100			100	100							800	400	5	2
444	5050	HOT	3300	2100	1000	400	1500	1200									800	500		
450	4890	PGI 0,2	300	125	200	75											100	50		
450	4940	HOT	1105	430	50	50	100	50	750	250							200	75	5	5
452	2000	PGI 0,2	26	16									1	1			25	15		
466	7160	HOT	240	82	200	50					15	10					20	20	5	2
471	2780	PGI 0,2	1	1															1	1
473	2650	PGI 0,2	1	1													1	1		
474	3810	ST 300	107	53	50	25					1	1	5	2			50	25	1	1
477	780	PGI 0,2	3	2	3	2														
489	1160	ST 300	111	61	50	30	50	25			10	5	1	1						
490	545	ST 300	5300	2100	1500	750	500	150	1000	650			800	100			1500	450		
491	1560	ST 300	761	381	50	25			100	100			10	5	1	1	600	250		
494	7280	ST 300	62	37	50	30					10	5			2	2				
497	6490	HOT	312	194	25	40	200	100			25	20	10	8	2	1	50	25		
517	8940	ST 300	121	55	5	2	100	40			10	10	5	2	1	1				
521	8780	ST 200	3	2	2	1									1	1				
550	4530	ST 200	20	7	15	5													5	2
649	8210	ST 600	32	21							2	1					20	10	10	10
661	5340	ST 600	75	135	20	15					40	100					15	20		
668	2640	HOT																		
716	3570	HOT	36	11	35	10							1	1						
724	2950	ST 600	10	6	5	3							5	3						
739	915	HOT	10100	3950	1000	500	100	50					1000	400			8000	3000		
741	440	ST 300	300	225	50	35							50	40	10	5	200	150		
758	2840	ST 600	23	13	20	10											2	1	1	2

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8. LIST OF DEEP-SEA STATIONS

This list comprises all the stations which were operated in water of 400 metres of depth or deeper. Excluded are here also the numerous stations at which observations on the productivity of phytoplankton were made; they are published by E. Steemann Nielsen & E. Aabye Jensen (1957).

Depth was recorded from echo-soundings, for details about method and corrections see Kiilerich (1959).

Hour is the local time of the ship which was corrected every day at noon; slight deviations from the time of the longitude may, therefore, occur. The hour given indicates the time at which the gear was calculated to have reached the bottom or the intended water layer. In the case of hydrography, however, only the time of starting the operations is indicated.

Gear. The abbreviation used are explained in the special list below.

Bottom. This is a very rough estimate of the character of the bottom deposits as judged from whatever material was brought up by the gear, and should not be taken as a detailed analysis of the sediments. Whenever possible, samples were preserved for a later examination by geologists; these samples have been deposited in the Geological Institute of the University of Copenhagen.

Estimated Fishing Depth, E. F. D., was calculated according to the formulae developed by Kullenberg (1951). No closing net was used, so E. F. D. indicates the depths at which the gear was towed and does not exclude a certain number of animals caught between the E. F. D. and the surface.

Wire out indicates the length of wire used for the particular gear; in the case of hydrographical observations two figures mean measurements carried out between the two levels.

Inclination of wire is the angle between the vertical and the wire; the first figure gives the value which according to Kullenberg (1951) should ensure contact between the gear and the bottom, while the two following figures are the extreme values of the actual readings carried out every fifth minute during the operation.

Speed in knots. This is not the speed of the ship, but the speed of the gear in relation to the bottom as calculated from Kullenberg's formulae.

Duration of haul was estimated from the readings of the inclination of the wire and should indicate the length of time in which the gear had contact with the bottom.

Length of haul in sea-miles was calculated from the estimates of the speed of the gear and the duration of the haul.

Remarks give partly a variety of irregularities about the operations and partly, in the case of the bottom-grabs, the volume brought up (litres), and in the case of the core-samples the length of the core (centimetres).

A number of meteorological observations was as usual entered in the ship's log, but these data, as also the direction of the haul, have been omitted here because they were considered of no general importance in the treatment of the collections of the animals.

In fig. 11 is given the route of the expedition with a selection of dates of the visits to a number of ports. The frames in this chart refer to the detailed charts on pp. 23-29 (pls. 1-4) in which the stations have been plotted.

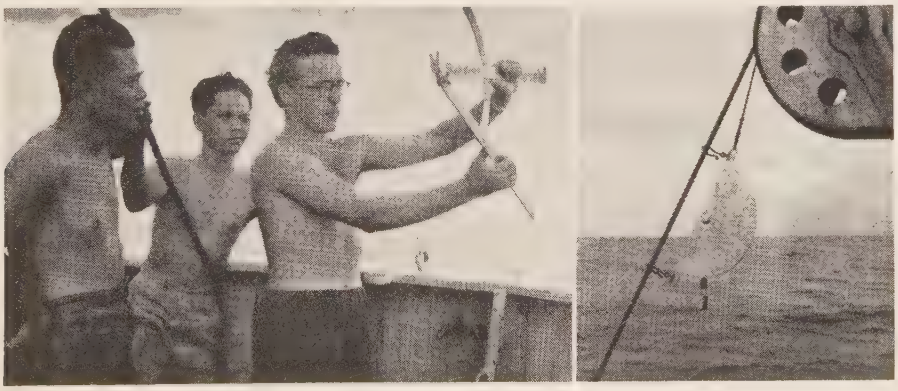


Fig. 10. Left: Gauging the angle while paying out.
Right: Angle gauge in position while trawling.

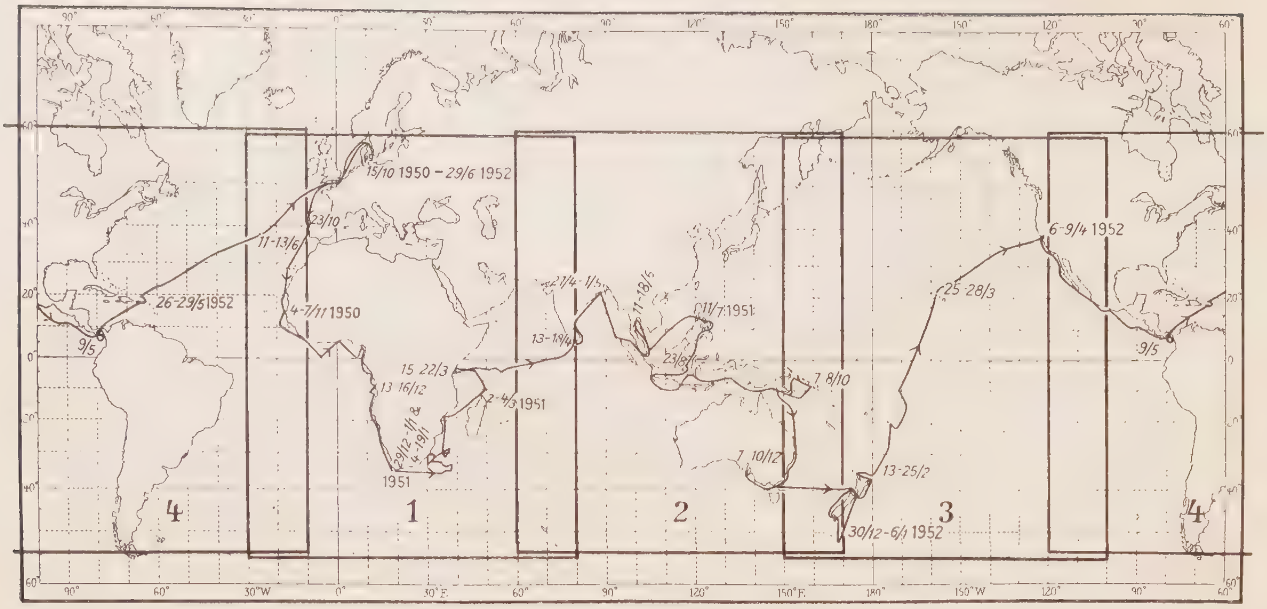
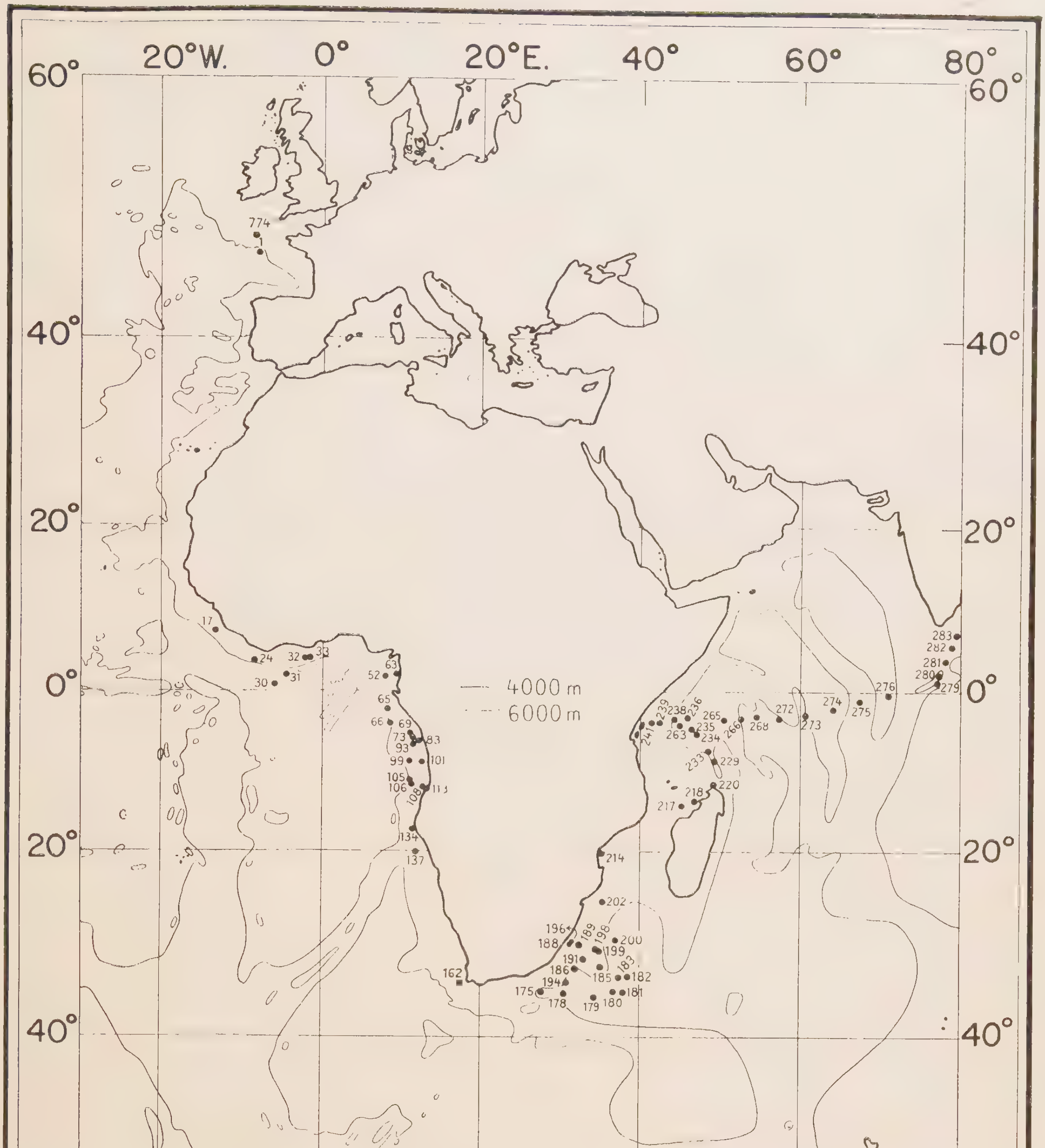


Fig. 11. The route of the expedition with a selection of dates of the visits to a number of ports. The frames refer to the detailed charts on pp. 23-29 (pls. 1-4).

List of Abbreviations

B T	Bathy-Thermograph, supplied by the Woods Hole Oceanographic Institution
D 45	Triangular Dredge, each side 45 cm
D 80	Rectangular Dredge, 80 × 30 cm
D O	Oyster Dredge
D R	Depth Recorder, supplied by the Woods Hole Oceanographic Institution
E. F. D.	Estimated Fishing Depth
H O T	Herring Otter Trawl of the type used by Danish fishermen. Length of the head-rope 32 m. Size of the meshes from 80 mm at the head to 14 mm in the cod-end. A bag made of canvas was attached to the inside of the cod-end to retain some of the fine bottom sediments and small animals
H Y D R	Hydrography
K C S	Kullenberg Core Sampler, one meter long
L L H	Long Lines with Halibut hooks
L L S	Long Lines with Shark hooks
P C S	Pfleger Core Sampler
P G 0.2	Petersen-Grab (Bottom Sampler) 0.2 sq.m
P G I 0.2	Petersen-Grab (Bottom Sampler) 0.2 sq.m, with two extra iron weights, each of 25 kg
S 100 C	Stramin Net, circular opening, diameter 100 cm. Stramin is a coarse canvas made of hemp, 400 strands to the meter
S 200 C	Stramin Net, circular opening, diameter 200 cm. Stramin as in S 100 C
S B T	Shrimp Beam Trawl, beam about 6 m.
S O T	Shrimp Otter Trawl of the type used by Danish fishermen (fig. 5). Length of head-rope 30 m. Size of meshes from 40 mm at the head to 16 mm in the cod-end. The cod-end lined inside with canvas as in the H O T
S S D	Shooting Star Dredge, magnetic rake, described by Bruun, Pauli & Langer (1955)
S T 100	Sledge Trawl, 1 m wide, of the Sigsbee-Agassiz-Monaco type. Single bag
S T 200	Sledge Trawl, 2 m wide. Single bag
S T 300	Sledge Trawl, 3 m wide. Single bag
S T 600	Sledge Trawl, 6 m wide (fig. 4). Two bags, each of the size used in the S T 300
T O T	Triangular Otter Trawl for pelagic fishing; of the type described by Parr (1934). Each of the three head-ropes was 13 m and each of the otter-boards was 110 cm long and 55 cm broad. Meshes 50 mm at the opening, 12 mm in cod-end to which was attached a canvas bag, 45 cm long.
V G	van Veen Grab (Bottom Sampler), 0.2 sq.m.

For literature references see p. 20.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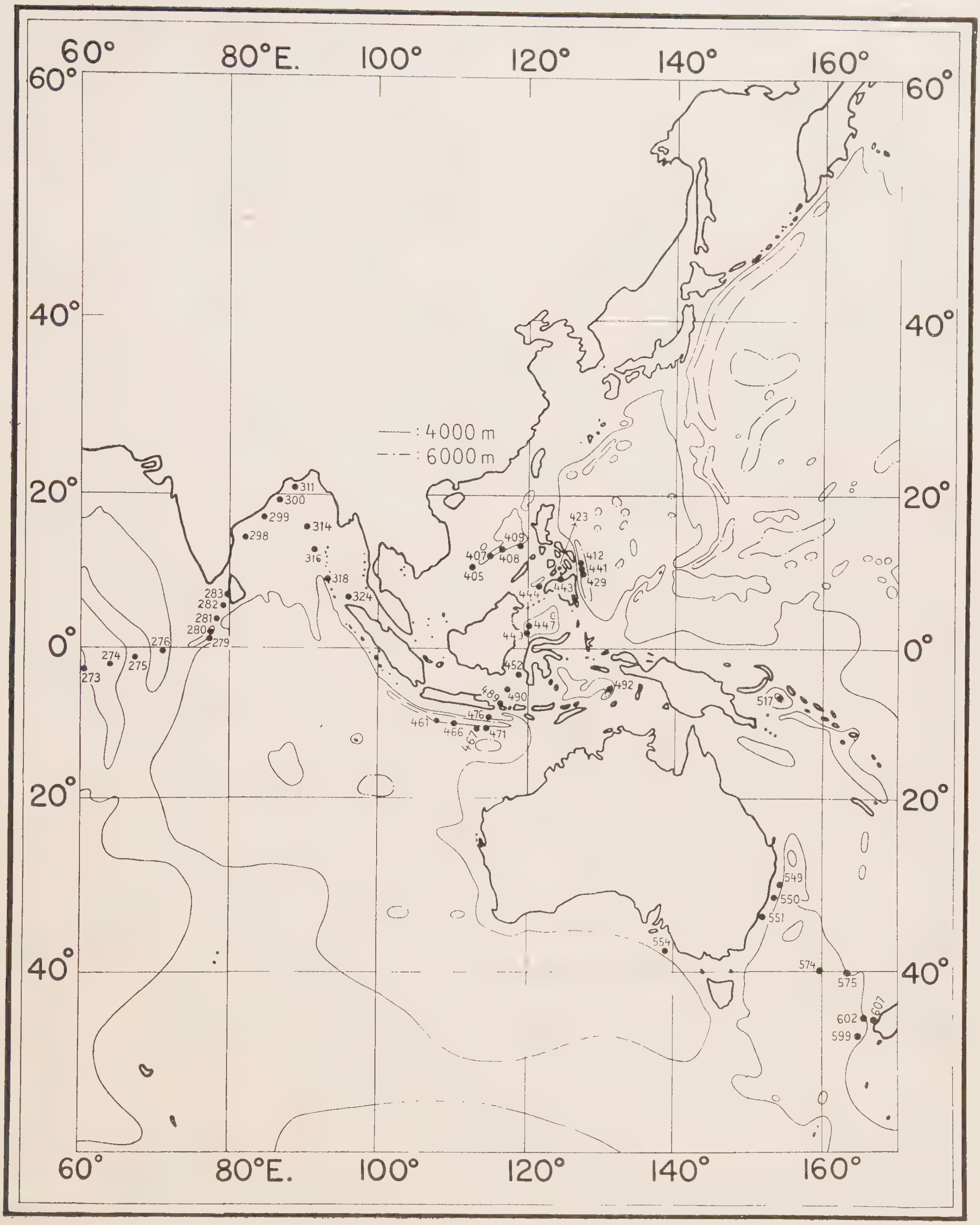
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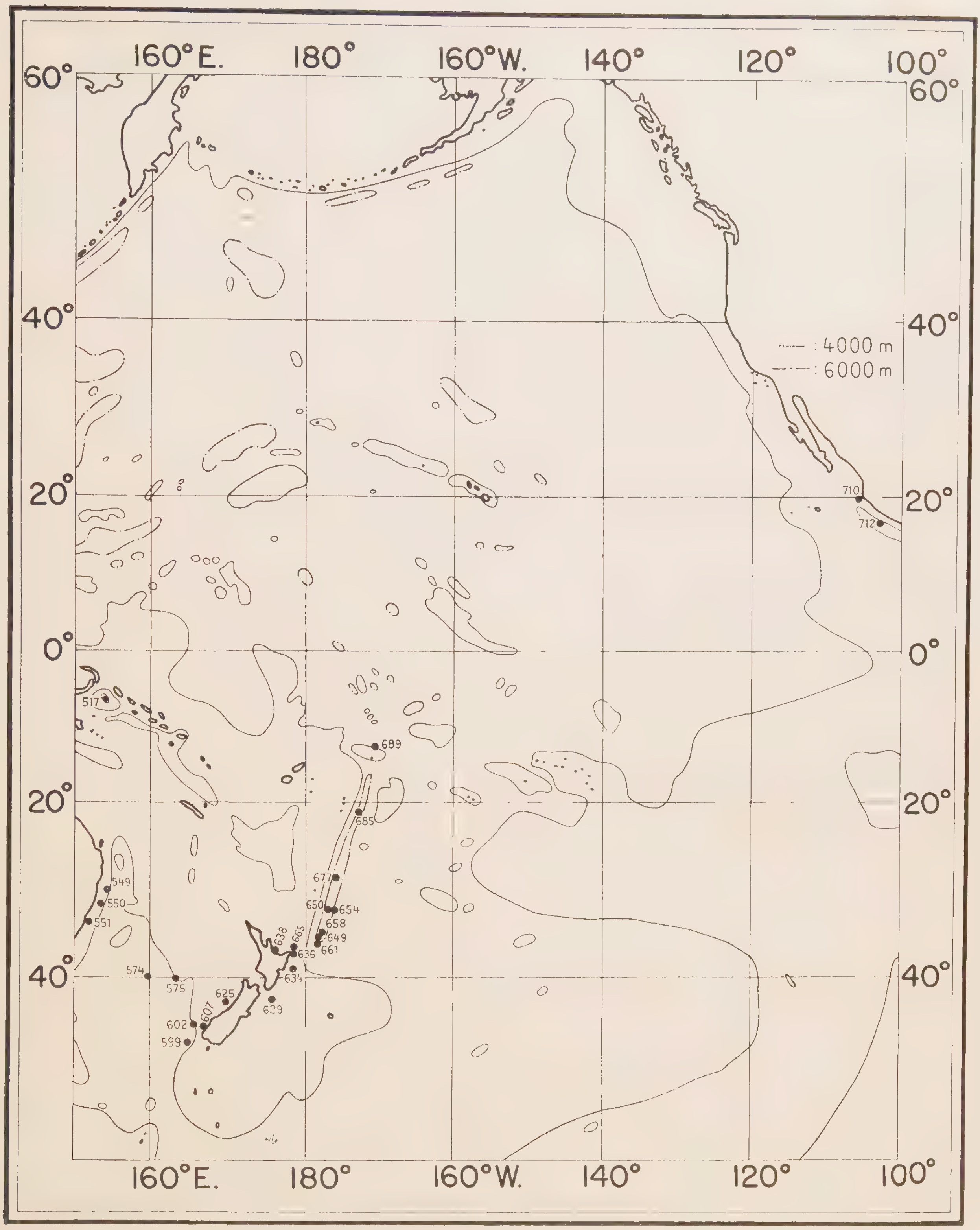
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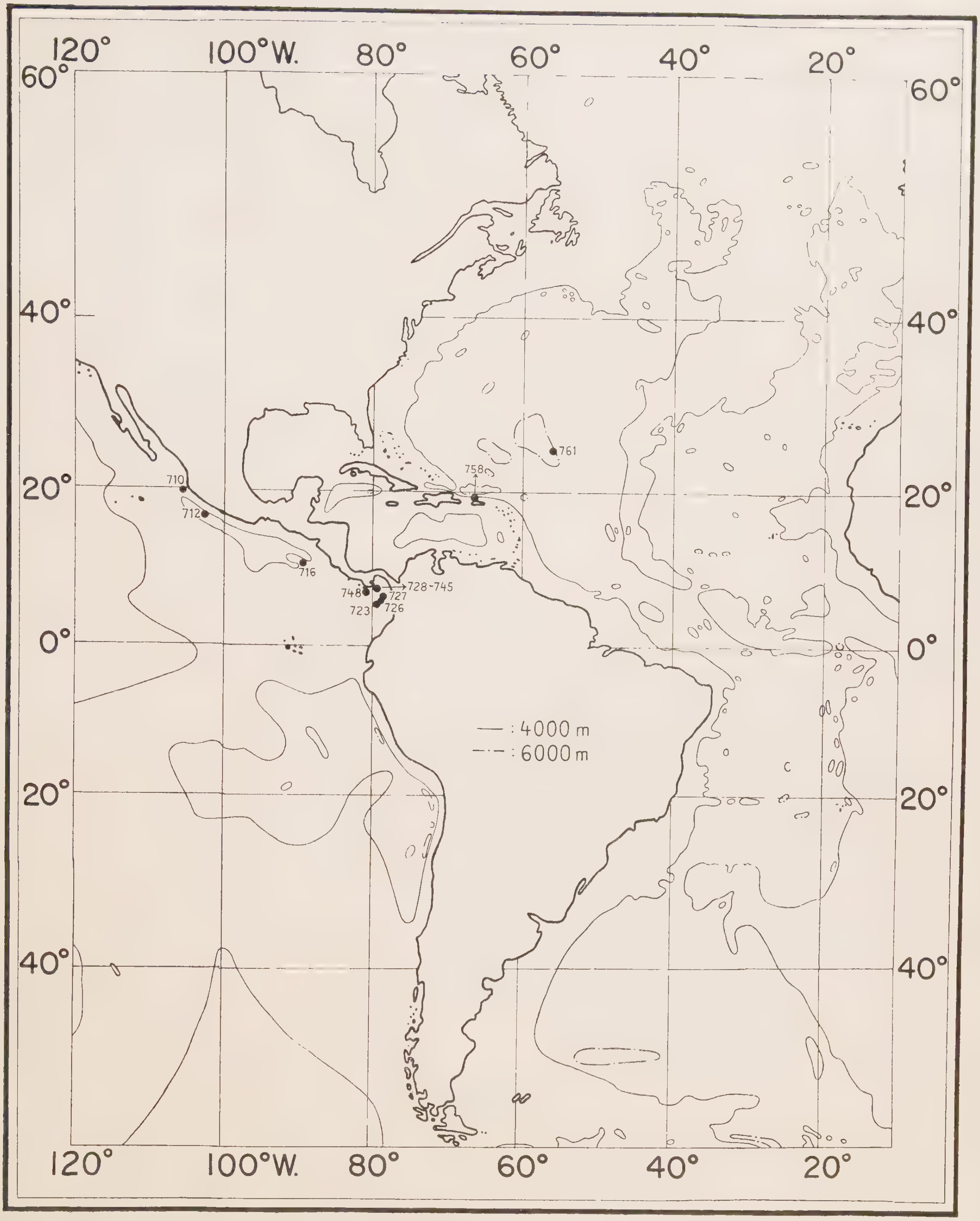
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Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
Atlantic Ocean				**1950**										
1	Bay of Biscay	46°28′N 8°01′W	4530	22.10.	8.30	HYDR	–	0–4500	–	–	0	405	–	–
17	Dakar-Monrovia	7°17′N 13°28′W	1260	10.11.	16.15	ST 100	mud	2000	–	40–47°	1.5	10	0.1	–
24	Monrovia-Takoradi	3°54′N 8°22′W	3200	15.11.	11.20	ST 300 + SSD	clay	4900	40°	47–58°	1.5–2	60	1.5	–
30	Monrovia–Takoradi	0°42′N 5°59′W	5160	18.11.	10.00	ST 300 + SSD	clay	7000	58°	58–63°	1.5	65	1.5	–
31	Monrovia–Takoradi	1°56′N 4°37′W	4930	19.11.	9.25	HYDR	–	0–4900	–	–	0	420	–	–
32	Monrovia–Takoradi	4°05′N 2°13′W	2100	20.11.	11.25	SBT	–	4000	43°	45–52°	2.2–2.5	180	6–7	–
33	Monrovia–Takoradi	4°00′N 1°43′W	1445	20.11.	17.30	PG 0,2	grey clay	1525	–	–	0	–	–	10 l.
52	San Tomé–Cameroon	1°42′N 7°51′E	2550	30.11.	12.00	SOT	muddy clay	4500	49°	50–52°	1.7	50	1.5	–
	San Tomé–Cameroon	1°42′N 7°51′E	2550	30.11.	17.45	HYDR	–	900	–	–	0	120	–	–
63	Off Gabon	2°00′N 9°14′E	1520	2.12.	12.35	SOT	blue clay	3500	38°	41–43°	2.2	70	2.3	bag lost
	Off Gabon	2°00′N 9°14′E	1500	2.12.	16.00	HYDR	–	0–1200	–	–	0	180	–	–
65	Off Gabon	2°17′S 8°10′E	2770	4.12.	11.20	ST 300 + SSD + D 45 + S 200 C	bluish clay	4500	50°	55–58°	1.8–2	60	1.8	bag of S 200 C lost
	Off Gabon	2°17′S 8°10′E	2610	4.12.	15.25	PG 0,2	bluish clay	2780	–	–	0	–	–	–
66	Off Gabon	4°00′S 8°25′E	4020	5.12.	10.25	ST 300 + SSD + D 45	greenish grey mud with Foraminifera	6300	50°	50–54°	2	60	2	net entangled in wire during lowering
	Off Gabon	4°00′S 8°25′E	4020	5.12.	10.25	+ S 200 C	–	5300	50°	50–54°	2	60	2	–
69	Off Congo River	5°18′S 11°08′E	1430	6.12.	22.15	HYDR	–	1440	–	–	0	360	–	–
	Off Congo River	5°18′S 11°08′E	1430	6.12.	23.10	PG 0,2	muddy clay	1550	–	–	0	–	–	23 l.
70	Off Congo River	5°17′S 11°18′E	1230	7.12.	1.30	HYDR	–	1220	–	–	0	150	–	–
	Off Congo River	5°17′S 11°18′E	1200	7.12.	4.20	PG 0,2	bluish clay	1360	–	–	0	–	–	33 l.

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
71	Off Congo River	5°23′S 11°28′E	880	7.12.	9.40	PG 0,2	muddy clay	990	–	–	0	–	–	23 1.; grab not released in first attempt
	Off Congo River	5°23′S 11°28′E	880	7.12.	10.00	HYDR	–	840	–	–	0	45	–	–
72	Off Congo River	5°31′S 11°25′E	790	7.12.	11.55	HYDR	–	750	–	–	0	110	–	–
	Off Congo River	5°39′S 11°19′E	735	7.12.	14.35	PG 0,2	mud and clay	850	–	–	0	–	–	33 1.
73	Off Congo River	5°41′S 11°26′E	450	7.12.	16.30	HYDR	–	435	–	–	0	55	–	–
	Off Congo River	5°41′S 11°26′E	430	7.12.	17.50	PG 0,2	muddy clay	465	–	–	0	–	–	11 1.
83	Off Congo River	6°02′S 12°12′E	800	8.12.	12.20	HYDR	–	725	–	–	0	52	–	–
	Off Congo River	6°02′S 12°12′E	750	8.12.	13.30	PG 0,2	–	850	–	–	0	–	–	not released
	Off Congo River	6°02′S 12°12′E	800	8.12.	14.05	PG 0,2	mud	870	–	–	0	–	–	45 1.
	Off Congo River	6°02′S 12°12′E	800	8.12.	14.40	HYDR	–	725	–	–	0	35	–	–
	Off Congo River	6°02′S 12°12′E	770	8.12.	15.25	PG 0,2	mud and clay	810	–	–	0	–	–	36 1.
93	Off Congo River	6°38′S 11°32′E	710	10.12.	8.10	HYDR	–	700	–	–	0	35	–	–
	Off Congo River	6°38′S 11°32′E	685	10.12.	9.15	PG 0,2	mud	800	–	–	0	–	–	25 1.
94	Off Congo River	6°48′S 11°19′E	990	10.12.	13.00	HYDR	–	980	–	–	0	30	–	–
	Off Congo River	6°48′S 11°19′E	960	10.12.	13.25	PG 0,2	muddy clay	1030	–	–	0	–	–	33 1.
95	Off Congo River	6°51′S 11°15′E	1170	10.12.	15.05	HYDR	–	1155	–	–	0	40	–	–
	Off Congo River	6°51′S 11°15′E	1150	10.12.	15.55	PG 0,2	muddy clay	1200	–	–	0	–	–	32 1.
96	Off Congo River	7°00′S 11°10′E	1510	10.12.	18.20	HYDR	–	1450	–	–	0	60	–	–
	Off Congo River	7°00′S 11°10′E	1435	10.12.	19.50	PG 0.2	mud	1620	–	–	0	–	–	31 1.
99	Off Angola	8°40′S 11°10′E	2690	11.12.	11.10	SOT	yellowish clay	5200	47°	48–50°	2	120	4	–
101	Off Angola	8°50′S 12°32′E	990	12.12.	9.00	ST 300	greenish mud	1800	48°	58–66°	1.6	50	1.5	bag filled with mud
	Off Angola	8°50′S 12°32′E	990	12.12.	12.00	LLH	–	1500	–	–	0	300	–	200 hooks
105	Loanda–Lobito	10°45′S 11°03′E	3980	17.12.	21.20	SOT	–	7000	49°	51–54°	2.1	140	–	trawl lost except one otter board

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
	Loanda–Lobito	10°45′S 11°03′E	4040	18.12.	3.45	HYDR	–	0–3900	–	–	0	320	–	–
	Loanda–Lobito	10°45′S 11°03′E	3980	18.12.	9.15	PG 0,2	clay	4100	–	–	0	–	–	not released (0,5 l.)
106	Loanda–Lobito	11°24′S 11°15′E	3660	18.12.	14.40	PG 0.2	clay	3850	–	–	0	–	–	20 l.
107	Loanda–Lobito	11°33′S 11°51′E	2370	18.12.	23.35	PG 0,2	clay	2500	–	–	0	–	–	18 l.
108	Loanda–Lobito	12°00′S 13°00′E	1470	19.12.	7.58	PG 0,2	clay	1560	–	–	0	–	–	20 l.
109	Loanda–Lobito	12°06′S 13°08′E	1190	19.12.	10.30	HYDR	–	1175	–	–	0	40	–	–
	Loanda–Lobito	12°06′S 13°08′E	1170	19.12.	11.20	PG 0,2	clay	1240	–	–	0	–	–	12 l.
110	Loanda–Lobito	12°05′S 13°08′E	975	19.12.	15.30	PG 0,2	clay	1040	–	–	0	–	–	19 l.
	Loanda–Lobito	12°05′S 13°08′E	975	19.12.	17.20	ST 300	clay	1800	48°	48–56°	1.6	30	0.8	–
112	Loanda–Lobito	12°16′S 13°17′E	735	20.12.	0.45	HYDR	–	730	–	–	0	–	–	–
	Loanda–Lobito	12°16′S 13°17′E	715	20.12.	1.15	PG 0,2	clay	740	–	–	0	–	–	20 l.
113	Loanda–Lobito	12°15′S 13°21′E	400	20.12.	2.15	PG 0,2	clay	410	–	–	0	–	–	18 l.
134	Off Kunene River, SW Africa	17°13′S 11°21′E	412	22.12.	12.50	PG 0,2	sand with glauconite	440	–	–	0	–	–	1.5 l.
135	Off Kunene River, SW Africa	17°13′S 11°16′E	710	22.12.	13.50	HYDR	–	710	–	–	0	20	–	–
	Off Kunene River, SW Africa	17°13′S 11°16′E	720	22.12.	14.25	PG 0,2	greenish sandy mud	725	–	–	0	–	–	18 l.
136	Off Kunene River, SW Africa	17°13′S 11°12′E	960	22.12.	15.40	PG 0,2	clay	1040	–	–	0	–	–	4 l.
137	Off SW Africa	20°04′S 11°56′E	537	23.12.	11.30	ST 300 + D 45 + D 80	–	–	36°	41–44°	–	–	–	–
			1951											
162	Off Cape Peninsula	34°11′S 17°36′E	–	2.1.	18.00	HYDR	–	480	–	–	0	15	–	–
175	Cape Town-Durban	35°00′S 27°22′E	4330	21.1.	9.40	PG 0,2	–	4640	–	–	0	–	–	contents washed out
	Cape Town-Durban	35°00′S 27°22′E	4390	21.1.	11.30	ST 300 + SSD + D 80	Globigerina ooze	6600	–	–	–	–	–	net and wire entangled

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
176	Cape Town-Durban	35°12′S 27°35′E	4350	21.1.	19.30	PG 0,2	–	4660	–	–	0	–	–	failed
	Cape Town-Durban	35°12′S 27°35′E	4350	21.1.	23.55	ST 300 + SSD + D 80	–	6600	52°	52-54°	1.8	60	1.8	–
177	Cape Town-Durban	35°13′S 27°45′E	4380	22.1.	4.00	HYDR	–	0–4450	–	–	0	420	–	–
	Cape Town-Durban	35°13′S 27°45′E	4380	22.1.	16.15	SOT	–	7200	50°	50–53°	2	75	2.2	–
178	Cape Town-Durban	35°07′S 30°35′E	4470	23.1.	12.00	ST 300 + SSD + D 80	clay	7000	53°	53–54°	1.8	15	0.3	bag of ST 300 lost, D 80 torn
	Cape Town-Durban	35°07′S 30°35′E	4470	23.1.	19.45	ST 300	–	6800	52°	52–53°	1.9	10	0.2	–
179	Cape Town-Durban	35°44′S 34°16′E	3800	24.1.	17.30	ST 300	–	6480	48°	50–54°	2.2	100	3.5	frame bent, hole in bag
180	Cape Town-Durban	34°56′S 36°31′E	5220	25.1.	12.45	ST 300	–	7450	58°	58–62°	1.7	90	2.5	–
	Cape Town-Durban	34°56′S 36°31′E	5220	25.1.	21.35	ST 300	–	7500	56°	59–61°	1.7	220	6	–
181	Cape Town-Durban	34°54′S 38°02′E	5380	26.1.	10.20	KCS	–	5515	–	–	0	130	–	86 cm
	Cape Town-Durban	34°54′S 38°02′E	5470	26.1.	13.00	HYDR	–	0–5350	–	–	0	415	–	–
182	Cape Town-Durban	33°28′S 38°32′E	5110–5340	27.1.	14.40	SOT + DR	–	7500	57°	59–62°	1.7	180	5	DR lost
183	Cape Town-Durban	33°25′S 37°20′E	5210	28.1.	14.00	S 200C	3000-3600 m.	5300	–	51–53°	1.8	140	4	–
184	Cape Town-Durban	33°06′S 35°21′E	1470	29.1.	16.00	VG 0,2	–	1580	–	–	0	–	–	failed
	Cape Town-Durban	33°06′S 35°21′E	1470	29.1.	17.00	KCS	–	1565	–	–	0	–	–	no bottom-material some Foraminifera
	Cape Town-Durban	33°06′S 35°21′E	1470	29.1.	17.40	HYDR	–	0–1475	–	–	0	110	–	–
	Cape Town-Durban	33°06′S 35°21′E	1300–1355	29.1.	21.00	ST 100	–	2600	38°	42–44°	2.3	60	2.3	bag torn
	Cape Town-Durban	33°06′S 35°21′E	1270–1425	30.1.	0.15	DO	–	2400	42°	42–45°	2	100	3.2	DO torn
185	Cape Town-Durban	32°31′S 35°01′E	1680	30.1.	11.00	LLH & LLS	–	650	–	–	0	60	–	160 hooks 150 lost
186	Cape Town-Durban	32°33′S 32°01′E	3620	31.1.	8.15	KCS	Globigerina ooze	3770	–	–	0	–	–	–
	Cape Town-Durban	32°33′S 32°01′E	3620	31.1.	9.50	HYDR	–	1500–3670	–	–	0	220	–	–
	Cape Town-Durban	32°33′S 32°01′E	3620	31.1.	16.45	SOT	Globigerina ooze	7000	45°	45–48°	2.3	45	0.8	net torn

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
188	Off Durban	29°55′S 31°13′E	440	2.2.	14.55	ST 300 + D 45 + D 80	–	1250	–	27°	–	60	–	gear not at bottom
	Off Durban	29°55′S 31°13′E	495	2.2.	17.35	KCS	–	–	–	–	0	–	–	3 attempts all without contents
	Off Durban	29°55′S 31°13′E	495	2.2.	20.35	ST 100	rocky (?)	1600	36°	36–38	–	40	–	bag lost
189	Off Durban	30°00′S 32°19′E	1580	3.2.	6.20	KCS	–	1630	–	–	0	40	–	2 attempts both without contents
190	Off Durban	29°42′S 33°19′E	2760	3.2.	14.10	KCS	Globigerina ooze	2950	–	–	0	40	–	sideways on bottom, empty
	Off Durban	29°42′S 33°19′E	2720	3.2.	16.55	ST 300	Globigerina ooze	4600	48°	48–50°	2	60	2	–
	Off Durban	29°42′S 33°19′E	2640	3.2.	22.05	ST 300	–	4600	47°	48–50°	2	110	3.8	trawl lost
191	Off Durban	31°49′S 32°52′E	3510	4.2.	18.30	KCS	clay with Foraminifera	–	–	–	0	–	–	62 cm
	Off Durban	31°49′S 32°52′E	3470	4.2.	21.35	ST 100 + D 45 + D 80	–	5250	51°	53–55°	1.8	100	3	gear not at bottom
192	Off Durban	32°00′S 32°41′E	3430	5.2.	7.05	ST 100 + D 45 + D 80	Globigerina ooze	6000	45°	48–52°	2.3	110	4	–
	Off Durban	32°00′S 32°41′E	3530	5.2.	16.20	SOT	Globigerina ooze	7200	44°	38–48°	2.4	55	2.2	–
193	Off Durban	32°34′S 31°52′E	3680	6.2.	7.30	KCS	Globigerina ooze	3780	–	–	0	–	–	36 cm
	Off Durban	32°34′S 31°52′E	3680	6.2.	11.35	SOT	Globigerina ooze	7400	45°	46–52°	2.3	55	2.2	–
194	Off Durban	34°09′S 30°45′E	4360	7.2.	6.40	KCS	Globigerina ooze	4480	–	–	0	–	–	almost empty
	Off Durban	34°09′S 30°45′E	4360	7.2.	11.10	SOT	Globigerina ooze	7500	50°	52–55°	2	80	2.3	–
	Off Durban	34°09′S 30°45′E	4360	7.2.	19.50	SOT	Globigerina ooze	7500	51°	51–56°	2	110	3.8	–
196	Off Durban	29°55′S 31°20′E	430	13.2.	21.30	PG 0,2	sand and clay	495	–	–	0	–	–	4 l.
	Off Durban	29°55′S 31°20′E	425	13.2.	22.50	ST 100	–	900	40°	40–50°	–	50	–	–
	Off Durban	29°55′S 31°20′E	430	14.2.	1.15	ST 300	sandy mud with stones	900 & 1200	38°	38–42°	–	100	–	–
197	Off Durban	29°57′S 31°26′E	495	14.2.	7.05	SOT	–	1450 & 1550	24°	24–25	-	70	–	–
	Of Durban	29°57′S 31°26′E	530	14.2.	10.35	SOT	–	1550	19°	19–26°	–	115	–	net lost
	Off Durban	29°57′S 31°26′E	620	14.2.	14.15	HYDR + BT	–	0–608	–	–	0	45	–	–

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
198	Off Durban	30°32′S 34°27′E	2690	15.2.	15.50	PG 0,2	–	2825	–	–	0	–	–	empty
	Off Durban	30°32′S 34°27′E	2700	15.2.	17.00	KCS	–	2780	–	–	0	–	–	empty
	Off Durban	30°32′S 34°27′E	2700	15.2.	20.10	ST 100 + D 80	–	4400	47°	49–52°	2	60	2	–
	Off Durban	30°32′S 34°27′E	2700	15.2.	23.30	ST 300 + SSD	–	2850	–	–	–	–	–	gear not at bottom
199	Off Durban	30°42′S 34°58′E	2370–2320	16.2.	6.00	S 200 C	1500-1700 m.	2875	–	45–50°	1.7	300	8.5	–
200	Off Natal	29°39′S 37°01′E	5020	17.2.	5.30	ST 300 + SSD + D 80	–	7400	56°	56–57°	1.8	10	–	gear not at bottom
	Off Natal	29°39′S 37°01′E	5070	17.2.	15.00	KCS	Globigerina ooze	5280	–	–	0	–	–	71 cm
	Off Natal	29°39′S 37°01′E	5090–4880	17.2.	20.45	HOT	–	7400	59°	59–62°	1.6	110	–	gear not at bottom
	Off Natal	29°39′S 37°01′E	5110	18.2.	5.00	HYDR	–	0–5200	–	–	0	670	–	–
	Off Natal	29°39′S 37°01′E	5110	18.2.	21.55	BT	–	7400	60°	63–66°	1.6	120	3	–
	Off Natal	29°39′S 37°01′E	5110	18.2.	21.55	HOT	–	3500	–	–	0	–	–	–
202	Off Natal	25°20′S 35 17′E	630	21.2.	10.20	VG 0,2	sand	710	–	–	0	–	–	2 l.
	Off Natal	25°20′S 35°17′E	595–575	21.2.	12.15	ST 300 + D 45 + D 80	–	1800	38°	38–39°	–	50	–	–
	Off Natal	25°20′S 35°17′E	590	21.2.	16.35	HOT	–	1500	35°	35–37°	–	55	–	–
203	Off Natal	25°36′S 35°21′E	730	21.2.	20.15	HOT	–	2200	32°	32–34°	–	35	–	–
214	Off Beira, Mozambique	20°12′S 35°15′E	380	24.2.	20.40	PG 0,2	clay	412	–	–	0	–	–	19 l.
215	Off Beira, Mozambique	20°12′S 35°15′E	720	24.2.	21.55	PG 0,2	clay	755	–	–	0	–	–	3 l.
	Off Beira, Mozambique	20°12′S 35°15′E	720	24.2.	22.15	HYDR	–	200–700	–	–	0	25	–	–
217	Mozambique Channel	14°20′S 45°09′E	3530	27.2.	9.00	KCS	clay	3625	–	–	0	–	–	34 cm.
	Mozambique Channel	14°20′S 45°09′E	3530	27.2.	9.45	HYDR + BT	–	0–3590	–	–	0	300	–	–
	Mozambique Channel	14°20′S 45°09′E	3390	27.2.	18.35	HOT	Globigerina ooze	6300	47°	48–53°	2	140	4.5	–
218	Mozambique Channel	13°41′S 46°40′E	3220	28.2.	12.25	BT	–	3050	–	–	0	60	–	–
	Mozambique Channel	13°41′S 46°40′E	3340	28.2.	19.00	TOT	450-650 m.	2000	–	25–29°	2.5	120	5	–

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
220	Off Cape Amber, Madagascar	11°43′S 49°09′E	1070–1360	1.3.	19.30	TOT	450-700 m.	2000	–	25–30°	2	150	5	–
229	Madagascar-Mombasa	8°40′S 49°25′E	4580	5.3.	20.00	KCS	–	4400	–	–	0	–	–	74 cm.
	Madagascar-Mombasa	8°40′S 49°25′E	4290	5.3.	20.55	HYDR + BT	–	0–4350	–	–	0	430	–	–
230	Madagascar-Mombasa	9°02′S 49°27′E	4860	7.3.	9.00	VG 0,2	–	5100	–	–	0	–	–	released but empty
	Madagascar-Mombasa	9°02′S 49°27′E	4940	7.3.	13.40	VG 0,2	Globigerina ooze	5160	–	–	0	–	–	7 l.
231	Madagascar-Mombasa	8°52′S 49°25′E	5020	7.3.	20.20	ST 300 + SSD + D 80	–	6600	60°	60–63°	1.5	60	1.6	–
	Madagascar-Mombasa	8°52′S 49°25′E	4480	8.3.	5.15	KCS	–	–	–	–	0	–	–	empty
232	Madagascar-Mombasa	9°03′S 49°22′E	4960	8.3.	10.20	HYDR	–	4250–4500	–	–	0	175	–	–
	Madagascar-Mombasa	9°03′S 49°22′E	4930	8.3.	17.15	HOT	–	7440	58°	59–62°	1.7	100	2.2	–
233	Madagascar-Mombasa	7°24′S 48°24′E	4730	9.3.	13.30	ST 300 + SSD + D 80	Globigerina ooze	6200	64°	64–65°	1.2	30	0.6	–
234	Madagascar-Mombasa	5°25′S 47°09′E	4800	10.3.	11.50	PG 0,2	Globigerina ooze	5010	–	–	0	–	–	16 l.
	Madagascar-Mombasa	5°25′S 47°09′E	4820	10.3.	17.05	HOT	–	7400	56°	56–60°	1.8	180	5.5	–
235	Madagascar-Mombasa	4°47′S 46°19′E	4810	11.3.	10.50	HOT	Globigerina ooze	7400	56°	57–62°	1.8	120	3.5	–
236	Madagascar-Mombasa	3°22′S 45°50′E	4770	12.3.	8.40	HYDR	–	4000–4250	–	–	0	255	–	–
237	Madagascar-Mombasa	2°18′S 45°18′E	4670	12.3.	18.10	TOT	450-750 m.	2500	–	21–27°	–	160	–	–
238	Off Kenya	3°23′S 44°04′E	3980	13.3.	9.55	PG 0,2	–	4160	–	–	0	–	–	at bottom but not released
	Off Kenya	3°23′S 44°04′E	3960	13.3.	14.30	HOT	Globigerina ooze	6900	50°	52–55°	2	190	6	–
239	Off Kenya	3°59′S 42°03′E	3290	14.3.	14.00	PG 0,2	Globigerina ooze	3450	–	–	0	–	–	8 l.
240	Off Kenya	4°32′S 41°26′E	2660	15.3.	1.10	PG 0,2	Globigerina ooze	2800	–	–	0	–	–	1.5 l.
	Off Kenya	4°32′S 41°26′E	2660	15.3.	2.30	HYDR	–	1000–2650	–	–	0	186	–	–
241	Off Kenya	4°00′S 41°27′E	1520	15.3.	11.40	PG 0,2	pure Globigerina	1610	–	–	0	–	–	6.5 l.
	Off Kenya	4°00′S 41°27′E	1510	15.3.	14.30	HOT	pure Globigerina	3400	–	–	2.1	100	6.5	net torn

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
242	Off Kenya	4°09′S 40°19′E	1015	16.3.	0.30	PG 0,2	clay with Globigerina	1090	–	–	0	–	–	2 l.
243	Off Kenya	4°09′S 40°19′E	665	16.3.	4.30	PG 0,2	clay with a little sand	760	–	–	0	–	–	6 l.
244	Off Kenya	4°09′S 40°19′E	400	16.3.	6.00	PG 0,2	corals in sand	420	–	–	0	–	–	2 l.
263	Mombasa-Seychelles	4°14′S 44°52′E	4620–4680	24.3.	15.40	TOT	800-1050 m.	3000	–	27–29°	ca. 3	230	10	–
265	Mombasa-Seychelles	3°30′S 50°20′E	5210	26.3.	14.00	BT	–	3500	–	–	0	15	–	–
266	Mombasa-Seychelles	3°38′S 52°43′E	4580	27.3.	6.00	HYDR	–	0–4500	–	–	0	510	–	–
	Mombasa-Seychelles	3°38′S 52°43′E	4580	27.3.	6.00	BT	–	3500	–	–	0	–	–	–
	Mombasa-Seychelles	3°38′S 52°43′E	4520	27.3.	17.15	PG 0,2	Globigerina ooze	4800	–	–	0	–	–	4 l.
	Mombasa-Seychelles	3°38′S 52°43′E	4700–4970	27.3.	21.15	TOT	3400-3800 m.	7000	–	39–43°	2.5–2.7	340	15	–
268	Mombasa-Seychelles	3°14′S 54°28′E	4020–4130	28.3.	18.20	TOT	350-550 m.	1600	–	26–30°	3	120	–	–
272	Seychelles-Ceylon	3°20′S 57°16′E	4060	2.4.	14.05	BT	–	1800	–	–	0	40	–	–
273	Seychelles-Ceylon	2°54′S 60°26′E	4220	3.4.	14.10	BT	–	2100	–	–	0	45	–	–
274	Seychelles-Ceylon	2°04′S 64°00′E	4350	4.4.	14.05	BT	–	2500	–	–	0	50	–	–
275	Seychelles-Ceylon	1°15′S 67°25′E	2470–2300	5.4.	14.45	BT	–	2500	–	–	0	50	–	–
276	Seychelles-Ceylon	0°42′S 71°07′E	4530	6.4.	8.30	HYDR	–	4500	–	–	0	150	–	wire broken, 5 water bottles lost
279	Seychelles-Ceylon	1°00′N 76°17′E	4330	8.4.	14.55	PG 0,2	Globigerina ooze	4600	–	–	0	–	–	13 l.
	Seychelles-Ceylon	1°00′N 76°17′E	4320	8.4.	19.50	ST 300 + SSD	–	5800	60°	60–62°	1.5	45	1.2	–
280	Seychelles-Ceylon	1°56′N 77°05′E	4350	9.4.	11.55	SOT	Globigerina ooze	7400	51°	51–53°	2	60	2	–
281	Seychelles-Ceylon	3°38′N 78°15′E	3310	10.4.	13.40	ST 300 + D 80	Globigerina ooze	4700	59°	59–61°	1.5	35	0.8	–
282	Seychelles-Ceylon	5°32′N 78°41′E	4040	11.4.	14.00	HOT	blackish mud	6800	51°	51–54°	2	80	2.8	–
283	Seychelles-Ceylon	7°05′N 79°37′E	920–880	12.4.	14.00	LLS + LLH	–	–	–	–	–	280	–	240 hooks

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
298	Bay of Bengal	14°20′N 82°00′E	3230	23.4.	13.15	TOT	1800-2200 m.	4900	–	30–36°	2.7–3.4	155	8	–
299	Bay of Bengal	17°10′N 84°30′E	2820	24.4.	17.25	HOT	mud	5300	46°	46–47°	2	30	1	–
300	Bay of Bengal	19°22′N 86°27′E	1545	25.4.	10.40	PG 0,2	–	1680	–	–	0	–	–	released, but empty
301	Bay of Bengal	19°30′N 86°32′E	1180	25.4.	16.00	PG 0,2	greenish mud	1300	–	–	0	–	–	3rd attempt success, 29 1.
	Bay of Bengal	19°30′N 86°32′E	1110	25.4.	18.10	TOT	700-800 m.	2100	–	29–31°	2.8	180	8.5	–
302	Bay of Bengal	19°42′N 86°48′E	1190	25.4.	23.00	ST 300	clay	2200	43°	43–44°	1.8	15	0.3	–
311	Off Ganges Delta	20°49′N 88°40′E	445	2.5.	6.35	PG 0,2	clay, a little sand	450	–	–	0	–	–	37 1.
312	Off Ganges Delta	20°16′N 88°59′E	700	2.5.	8.30	PG 0,2	clay and mud	710	–	–	0	–	–	36 1.
314	Bay of Bengal	15°54′N 90°17′E	2600	3.5.	19.05	HOT	brownish ooze	4800	47°	47–49°	2	60	2	–
316	Bay of Bengal	12°43′N 91°17′E	3170	4.5.	17.15	TOT	1700-1900 m.	4500	–	31–34°	3	180	9	–
318	Bay of Bengal	9°02′N 93°07′E	1440	5.5.	19.15	TOT	800-1100 m.	2800	–	27–32°	3	180	9	–
324	Strait of Malaca	6°38′N 96°00′E	1140	9.5.	13.00	ST 300	brownish Globigerina ooze	2100	48°	50–54°	1.7	35	1	–
405	South China Sea	10°25′N 112°37′E	2910	2.7.	11.45	PG 0,2	Globigerina ooze	3060	–	–	0	–	–	21 1.
406	South China Sea	10°34′N 112°51′E	2310	2.7.	16.10	TOT	1850-2150 m.	4500	–	35–37°	2.2–2.25	160	6.5	–
	South China Sea	10°34′N 112°51′E	2310	2.7.	20.20	HYDR + BT	–	1550–2300	–	–	–	80	–	no BT recording
407	South China Sea	12°10′N 114°56′E	4390	3.7.	11.00	HYDR	–	0–4400	–	–	–	330	–	–
	South China Sea	12°10′N 114°56′E	4390	3.7.	11.00	BT	–	3000	–	–	–	–	–	–
	South China Sea	12°10′N 114°56′E	4390	3.7.	19.00	TOT	3400-3800 m.	5300	–	50–55°	1.5	180	4.5	–
408	South China Sea	12°47′N 116°24′E	4330	4.7.	11.00	ST 300	Globigerina ooze	6600	54°	54–56°	1.5	120	3	–
	South China Sea	12°47′N 116°24′E	4330	4.7.	17.00	PG 0,2	Globigerina ooze	4530	–	–	0	–	–	not released
409	South China Sea	13°44′N 118°56′E	3780–3850	5.7.	9.00	TOT	1600-2000	2900	–	44–52°	1.5	180	4.5	–
412	Philippine Trench	11°13′N 126°21′E	8870	12.7. 13.7.	18.10	HYDR	–	0–9150	–	–	0	1020	–	–
	Philippine Trench	11°13′N 126°21′E	8990	13.7.	16.10	PG 0,2	clay and sand	9300	–	–	0	–	–	125 cc.

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
413	Philippine Trench	10°20′N 126°36′E	8600	15.7.	1.15	KCS	–	9000	–	–	0	–	–	empty
	Philippine Trench	10°20′N 126°36′E	10060	15.7.	7.30	KCS	–	10480	–	–	0	–	–	75 cm.
	Philippine Trench	10°20′N 126°36′E	10010	15.7.	21.00	PG 0,2	clay	10470	–	–	0	–	–	not released, clay on gear
417	Philippine Trench	10°20′N 126°38′E	9200–8380	20.7.	18.00 21.45	PG 0,2	–	9400 & 8900	–	–	0	–	–	not released
418	Philippine Trench	10°13′N 126°43′E	10190–10150	21.7.	19.15	ST 300 + D 80 + S 100 C	clay with gravel and stones	12160	74°	74–76°	1	90	1.5	–
419	Philippine Trench	10°19′N 126°39′E	10150–10210	22.7.	21.30	ST 300 + D 80 + S 100 C	clay	12220	74°	74–76°	1	120	2	S 100 C lost
420	Philippine Trench	10°24′N 126°40′E	10170	23.7.	18.15	PG 0,2	–	10700	–	–	0	–	–	not released
421	W of Philippine Trench	10°26′N 126°05′E	1000	24.7.	4.00	PGI 0,2	clay	1025	–	–	0	30	–	15 l.
422	W of Philippine Trench	10°47′N 126°02′E	2040	24.7.	8.30	PGI 0,2	clay	2035	–	–	0	90	–	26 l.
	W of Philippine Trench	10°47′N 126°02′E	2100	24.7.	10.30	KCS	–	2350	–	–	0	–	–	empty
423	E of Cebu, Philippines	10°27′N 124°18′E	810	25.7.	2.50	PGI 0,2	green mud	832	–	–	0	–	–	31 l.
	E of Cebu, Philippines	10°27′N 124°18′E	750	25.7.	5.35	ST 300	green mud	2200	36°	50–60°	2	10	0.3	–
424	Philippine Trench	10°28′N 126°39′E	10120	27.7.	20.55	PGI 0,2	brownish clay covering blackish green sand	11100	–	–	–	–	–	26 l.
429	Philippine Trench	9°49′N 126°44′E	10020–10120	2.8.	22.10	ST 300 + D 45 + D 80	clay	11940	73°	73–75°	1	5–120	–	gear entangled in wire, 500 m.
430	Philippine Trench	10°20′N 126°37′E	10020	3.8.	8.15	HYDR	–	8000–10270	–	–	0	345	–	bottles not released
	Philippine Trench	10°20′N 126°37′E	10040	3.8.	14.00	HYDR	–	1000–10270	–	–	0	330	–	bottles not released
	Philippine Trench	10°20′N 126°37′E	10060	3.8.	19.30	HYDR	–	8000–10270	–	–	–	360	–	bottles not released
431	Philippine Trench	10°21′N 126°38′E	10030	4.8.	11.00	HYDR	–	8000–10270	–	–	–	930	–	–
433	Philippine Trench	9°51′N 126°51′E	10000	5.8.	23.15	HYDR	–	4000–10250	–	–	0	945	–	–
434	Philippine Trench	10°04′N 126°44′E	9580–9530	7.8.	5.15	ST 300 + D 45 + D 80	–	11700	73°	73–74°	1	120	2	gear not at bottom

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
435	Philippine Trench	10°20′N 126°41′E	9820–10000	7.8.	20.10	ST 300 + D 45 + D 80	very stiff clay	11900	72°	72–73°	1	100	1.7	ST 300 entangled in wire, 300 m.
	Philippine Trench	10°20′N 126°41′E	9980	8.8.	4.20	HYDR + KCS	–	10615	–	–	0	630	–	core sample lost at surface
436	E of Cebu, Philippines	10°12′N 124°14′E	710	9.8.	7.30	ST 300 + D 45 + D 80	green mud	2000	35°	35–39°	1.8–2	50	1.7	–
440	Philippine Trench	10°25′N 126°40′E	10020	14.8.	9.00	HYDR + KCS	clay	3250–10610	–	–	0	540	–	KCS: 74 cm. the lower 4 cm. disturbed
441	Philippine Trench	10°26′N 126°40′E	10040	14.8.	20.00	ST 300 + D 45 + D 80	–	11770	–	–	–	–	–	no echo sounding, gear not at bottom
443	Mindanao Sea	8°48′N 124°09′E	1500	16.8.	22.30	ST 300 + D 45 + D 80	mud, many fragments of plants	2700	46°	46°	1.5	20	0.4	–
444	Sulu Sea	7°54′N 121°30′E	5050	17.8.	21.35	HOT	mud, many fragments of plants	8000	56°	57–60°	1.6	55	1.5	–
445	Sulu Sea	7°45′N 121°34′E	4980	18.8.	2.30	HYDR + KCS	–	0–5190	–	–	–	330	–	KCS: 75 cm.
	Sulu Sea	7°45′N 121°34′E	4980	18.8.	2.30	BT	–	1500	–	–	–	–	–	–
447	Celebes Sea	3°05′N 120°10′E	4660	20.8.	13.45	PGI 0,2	brownish clay	5000	–	–	0	–	–	51 1.
448	Celebes Sea	2°54′N 120°04′E	4600	20.8.	18.45	TOT + DR	1700-2200 m.	4200	–	37–40°	2	120	4	–
449	Celebes Sea	2°13′N 119°42′E	5160	21.8.	2.30	HYDR + KCS	–	0–5375	–	–	0	425	–	KCS: 81 cm.
	Celebes Sea	2°13′N 119°42′E	5160	21.8.	2.30	DR	–	2000	–	–	0	–	–	–
450	Celebes Sea	1°50′N 119°20′E	4940–4970	21.8.	13.20	HOT	–	9700	47°	50–57°	2	100	3.7	bag torn
	Celebes Sea	1°50′N 119°20′E	4890	21.8.	23.50	PGI 0,2	bluish clay with fragments of plants	5220	–	–	–	–	–	39 1.
452	Makassar Strait	3°37′S 118°34′E	2000	24.8.	11.00	PGI 0,2	greenish clay	2150	–	–	0	–	–	32 1.
453	Makassar Strait	3°56′S 118°26′E	2000	24.8.	15.20	ST 300 + D 45 + D 80	greenish clay	3500	48°	48–50°	1.5	65	1.6	–
	Makassar Strait	3°56′S 118°26′E	1990	24.8.	18.00	HYDR + KCS	–	0–2140	–	–	0	230	–	KCS: 56 cm.
461	Sunda Trench	10°05′S 107°54′E	6810	3.9.	5.00	ST 300 + D 45 + D 80	–	9750	59°	59–61°	1.5	115	3	gear not at bottom

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
462	Sunda Trench	10°02′S 107°52′E	6730	3.9.	14.45	PGI 0,2	bluish clay	7400	–	–	0	–	–	16 l.
463	Sunda Trench	10°16′S 109°51′E	7130	4.9.	7.00	HYDR + KCS	–	0–7440	–	–	0	675	–	core sample lost at surface
464	Sunda Trench	10°18′S 109°38′E	7150– 6200	4.9.	22.10	ST 300 + D 45 + D 80	–	10200	59°	59–60°	1.5	90	2.2	gear not at bottom
465	Sunda Trench	10°20′S 109°55′E	7000– 6900	5.9.	13.50	ST 300 + D 45 + D 80	–	10300	59°	61–64°	1.5	180	4.5	bag of ST 300 lost
466	Sunda Trench	10°21′S 110°12′E	7160	6.9.	8.35	HOT	bluish clay	10600	60°	61–62°	1.5	125	3	–
467	Sunda Trench	10°46′S 113°06′E	5110	8.9.	5.30	KCS	–	5440	–	–	0	180	–	empty
468	Sunda Trench	10°55′S 113°06′E	4700	8.9.	9.30	PGI 0,2	–	5140	–	–	0	–	–	not quantitative, 25 cc.
	Sunda Trench	10°55′S 113°06′E	4750	8.9.	13.15	KCS	–	4985	–	–	0	–	–	core sample lost at surface
469	Sunda Trench	10°51′S 113°10′E	5020	8.9.	15.55	PGI 0,2	–	5350	–	–	0	–	–	1 l.
470	Sunda Trench	11°04′S 113°34′E	5210– 5130	9.9.	1.45	ST 300 + D 45 + D 80	–	8000	54°	56–58°	1.5	80	2	gear not at bottom
471	Sunda Trench	10°26′S 114°15′E	2820	9.9.	18.00	KCS	–	3150	–	30–90°	0	–	–	empty
	Sunda Trench	10°26′S 114°15′E	2780	9.9.	21.30	PGI 0,2	clay	3025	–	–	0	–	–	25 l.
	Sunda Trench	10°26′S 114°15′E	2990– 2810	10.9.	1.25	ST 300 + D 45 + D 80	clay and vulcanic tuff	4900	50°	52–58°	1.6	90	2.4	bag of ST 300 torn
472	Sunda Trench	10°24′S 114°07′E	2250– 2030	10.9.	11.20	HOT	800-900 m.	3600	–	–	3	100	5	gear not at bottom
473	Sunda Trench	10°16′S 113°57′E	2650	10.9.	19.10	PGI 0,2	–	3030	–	–	0	–	–	almost all bottom material washed out
474	Sunda Trench	9°49′S 114°13′E	3840– 3810	11.9.	5.15	ST 300 + D 45 + D 80	–	6100	52°	54–57°	1.5	90	2.2	–
476	S of Bali	9°04′S 114°43′E	1555	11.9.	19.25	PG 0,2	clay with fine sand	1675	–	–	0	–	–	6.5 l.
477	S of Bali	9°01′S 114°48′E	780	11.9.	21.30	PG 0,2	sandy clay	810	–	–	0	–	–	12 l.
478	S of Bali	8°50′S 114°55′E	600	12.9.	0.25	PG 0,2	sandy clay	625	–	–	0	–	–	21 l.

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
480	S of Bali	8°49′S 115°00′E	440	12.9.	2.35	PG 0,2	sand, a little clay	470	–	–	0	–	–	20 l.
489	Bali Sea	7°38′S 116°08′E	1160	13.9.	16.15	ST 300 + D 45 + D 80	dark clay	1950	59°	59–60°	1	60	1	–
490	Bali Sea	5°25′S 117°03′E	570–545	14.9.	9.40	ST 300 + D 45 + D 80	sand and clay	1300	39°	39–45°	1.5	60	1.5	–
491	Makassar Strait	4°56′S 117°39′E	1560	14.9.	20.00	ST 300 + D 45 + D 80	muddy clay	2800	48°	50–52°	1.6	60	1.6	–
492	Banda Trench	5°31′S 131°01′E	7250	20.9.	3.45	PGI 0,2	green clay	7650	–	–	0	–	–	not released
	Banda Trench	5°31′S 131°01′E	7250	20.9.	6.45	HYDR + KCS	–	0–7680	–	–	0	615	–	KCS: 59 cm.
	Banda Trench	5°31′S 131°01′E	7240	20.9.	6.45	BT	–	3600	–	–	0	–	–	–
494	Banda Trench	5°36′S 131°01′E	7280	21.9.	13.05	ST 300 + D 45 + D 80	–	10300	60°	60–63°	1.5	130	3	gear not at bottom
	Banda Trench	5°36′S 131°01′E	7240–7290	22.9.	0.00	ST 300 + D 45 + D 80	clay	10400	60°	64°–72°	1.5	125	3	–
495	Banda Trench	5°26′S 130°58′E	7290–7250	22.9.	15.45	HOT	clay	11200	58°	60–62°	1.5	120	3	–
496	Banda Trench	5°36′S 131°06′E	7270	23.9.	4.30	PGI 0,2	soft clay	7765	–	–	0	–	–	6.5 l.
497	Banda Trench	5°18′S 131°18′E	6490–6650	23.9.	20.00	HOT	soft clay	9800	59°	59–61°	1.5	125	3	–
499	Banda Trench	5°21′S 131°17′E	6580	24.9.	17.50	PGI 0,2	greenish clay	6950	–	–	0	–	–	43 l.
517	New Britain Trench	6°31′S 153°58′E	8820	11.10.	5.50	HYDR + KCS	clay	0–9500	–	–	0	755	–	KCS: 47 cm.
	New Britain Trench	6°31′S 153°58′E	8840	11.10.	21.55	PGI 0,2	clay	9200	–	–	0	–	–	content almost totally washed out
	New Britain Trench	6°31′S 153°58′E	8850	12.10.	8.15	HYDR	–	0–5000	–	–	–	265	–	–
	New Britain Trench	6°31′S 153°58′E	8810	12.10.	8.15	BT	–	1800	–	–	–	–	–	no recording
	New Britain Trench	6°31′S 153°58′E	8940	13.10.	3.25	ST 300 + D 45 + D 80	–	11100	70°	73–74°	1.2	155	3	D 80 lost
	New Britain Trench	6°31′S 153°58′E	8720	13.10.	16.05	PGI 0,2	clay	9255	–	–	0	–	–	20 l.
518	New Britain Trench	6°11′S 153°31′E	8800	14.10.	2.00	ST 300 + D 45 + D 45	–	11100	–	–	–	–	–	gear not at bottom

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
519	New Britain Trench	6°12′S 153°43′E	8950	15.10.	4.50	ST 300 + D 45 + D 45	–	11100	70°	72–75°	1.2	120	2	gear not at bottom
520	New Britain Trench	6°10′S 153°42′E	c. 7800	15.10.	18.00	ST 300 + D 45 + D 45	–	5000	–	–	–	–	–	no echo, gear not at bottom
521	New Britain Trench	5°59′S 153°28′E	8830–8780	16.10.	9.50	ST 200	clay	11600	67°	71–73°	1.4	150	3.5	–
549	Coral Sea	30°05′S 154°33′E	1560	11.11.	21.50	PGI 0,2	–	1710	–	–	0	–	–	not released
550	Tasman Sea	31°27′S 153°33′E	4090	12.11.	12.00	PGI 0,2	very stiff clay	4345	–	–	0	–	–	12 1.
	Tasman Sea	31°27′S 153°33′E	4530	12.11.	21.40	ST 200 + D 45 + SSD	very stiff clay	6000	62°	69–75°	1.3	120	2.6	–
551	Off Sydney	33°42′S 151°51′E	680–760	13.11.	20.00	TOT	ca. 500 m.	1500	–	29–32°	2	180	6	–
554	Great Australian Bight	37°28′S 138°55′E	1340–1320	5.12.	19.00	ST 300 + D 45	Globigerina ooze	2500	45°	52–56°	1.5	70	1.7	–
	Great Australian Bight	37°28′S 138°55′E	1360	5.12.	22.00	PGI 0,2	–	1550	–	–	0	–	–	released before reaching bottom
555	Great Australian Bight	37°21′S 138°44′E	875	6.12.	0.05	PGI 0,2	clay, a little sand	955	–	–	0	–	–	3.5 1.
556	Great Australian Bight	37°18′S 138°43′E	795	6.12.	0.30	PGI 0,2	clay	750	–	–	0	–	–	9 1.
557	Great Australian Bight	37°13′S 138°42′E	680	6.12.	1.30	PGI 0,2	clay	455	–	–	0	–	–	5 1.
574	Tasman Sea	39°45′S 159°39′E	4670	18.12.	13.40	ST 600 + SSD	–	7500	53°	57–62°	1.7	130	3.6	–
575	Tasman Sea	40°11′S 163°35′E	3710	19.12.	13.35	SOT	pteropod ooze	7500	45°	47–50°	2	115	4	–
	Tasman Sea	40°11′S 163°35′E	3690	19.12.	18.30	HYDR + KCS	–	1250–4000	–	–	0	195	–	KCS at bottom but empty
		1952												
599	Tasman Sea	45°47′S 164°39′E	4390	13.1.	17.45	ST 300 + D 45 + SSD	–	6080	58°	65–69°	1.4	150	3.5	–
600	Tasman Sea	45°46′S 164°34′E	4420	14.1.	0.15	PGI 0,2	Globigerina ooze	4730	–	–	0	–	–	not quantitative

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
601	Tasman Sea	45°51′S 164°32′E	4400	14.1.	7.45	HOT	Globigerina ooze	7500	53°	55–60°	1.7	120	3.5	–
	Tasman Sea	45°51′S 164°32′E	4360	14.1.	14.00	HYDR + KCS	–	0–4625	–	–	0	375	–	KCS empty
602	Tasman Sea	43°58′S 165°24′E	4510	15.1.	17.35	ST 300 + D 45 + D 80	bluish clay	6300	60°	66–70°	1.3	135	3	–
607	Tasman Sea	44°18′S 166°46′E	3830	17.1.	17.15	VG 0,2	–	4130	–	–	0	–	–	released before reaching bottom
	Tasman Sea	44°18′S 166°46′E	3580	17.1.	23.30	HOT	clay	6600	50°	51–58°	1.7	90	2.5	–
625	Tasman Sea	42°08′S 170°20′E	610	20.1.	15.05	KCS	Globigerina ooze	630	–	–	0	20	–	45 cm.
626	Tasman Sea	42°10′S 170°10′E	610	20.1.	16.00	PGI 0,2	Globigerina ooze	630	–	–	0	–	–	13 1.
	Tasman Sea	42°10′S 170°10′E	610	20.1.	18.00	ST 300	Globigerina ooze	1500	–	41–50°	1.5	65	1.5	–
	Tasman Sea	42°10′S 170°10′E	610	20.1.	21.45	HOT	Globigerina ooze	1500	–	30°	2.5	60	2.5	–
629	E of Cook Strait	41°46′S 175°48′E	c.2000	24.1.	22.00	TOT+DR	1100-1300 m.	1700	–	42–48°	1.5	110	3	–
634	Wellington-Auckland	39°05′S 178°20′E	1400	25.1.	21.10	TOT+DR	1000-1200 m.	1700	–	37–41°	–	110	–	–
636	Wellington-Auckland	37°24′S 178°24′E	–	26.1.	10.50	PGI 0,2	–	1400	–	–	0	–	–	no echo, gear not at bottom
638	Wellington-Auckland	37°33′S 175°57′E	660	26.1.	16.55	PGI 0,2	clay with a little sand	685	–	–	0	–	–	31 1.
649	Kermadec Trench	35°16′S 178°40′W	8210–8300	14.2.	0.05	ST 600	grey clay with pumice	11700	60°	60–65°	1.6	115	3	–
650	Kermadec Trench	32°20′S 176°54′W	6620–6730	15.2.	23.35	ST 600	brown clay with pumice	9400	59°	61–64°	1.5	135	3.4	–
651	Kermadec Trench	32°10′S 177°14′W	6960–7000	16.2.	12.55	HOT	brown clay with pumice	11600	54°	54–56°	1.9	35	1	–
652	Kermadec Trench	32°07′S 176°48′W	6030–5950	17.2.	3.10	HOT	–	10600	51°	–	2	15	0.5	gear not at bottom
653	Kermadec Trench	32°09′S 176°35′W	6180	17.2.	19.20	HOT	brown clay with pumice	10800	51°	51–52°	2	35	1.2	–
654	Kermadec Trench	32°10′S 175°54′W	5850–5900	18.2.	12.45	HOT	brown clay with pumice	10500	50°	50–54°	2	100	3.3	net partly torn
656	Kermadec Trench	35°20′S 178°55′W	7640 7680	20.2.	6.05	ST 600	–	10600	61°	61–63°	1.5	70	1.8	–
658	Kermadec Trench	35°51′S 178°31′W	6660–6770	20.2.	22.45	ST 600	brown sand with clay and stones	9900	57°	60–64°	1.5	135	3.6	net partly torn

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
659	Kermadec Trench	35°30′S 178°46′W	7840	21.2.	20.15	ST 600	–	11200	59°	61–63°	1.6	120	3.2	gear not at bottom
660	Kermadec Trench	35°35′S 178°51′W	7800–7310	22.2.	11.15	ST 600	–	11200	59°	61–64°	1.6	120	3.2	gear not at bottom
661	Kermadec Trench	36°07′S 178°32′W	5340–5230	23.2.	2.40	ST 600	pumice in abundance	8500	53°	56–62°	1.7	125	3.5	–
662	Kermadec Trench	36°22′S 178°23′W	4630	23.2.	13.25	HOT	–	9100	44°	44–47°	2.2	80	3	gear not at bottom
663	Kermadec Trench	36°31′S 178°38′W	4410	24.2.	0.30	HOT	brown sandy clay with pumice	9000	44°	46–50°	2.2	125	4.5	–
664	Kermadec Trench	36°34′S 178°57′W	4540	24.2.	11.30	HOT	brown sandy clay with pumice	8900	46°	46–51°	2.1	120	4.2	–
665	Kermadec Trench	36°38′S 178°21′E	2470	25.2.	7.40	HOT	grey clay	5600	41°	41–44°	2	100	3.3	bag lost
668	Kermadec Trench	36°23′S 177°41′E	2640	29.2.	1.50	HOT	clay	5000	47°	48–51°	2	75	2.5	–
677	Kermadec Trench	28°38′S 175°53′W	9130	4.3.	10.45	HYDR + PCS	–	6910–9715	–	–	–	390	–	PCS at bottom, but empty
	Kermadec Trench	28°38′S 175°53′W	9190	4.3.	20.00	HYDR + PCS	clay	0–9760	–	–	0	610	–	PCS: 30 cm.
685	Tonga Trench	21°06′S 173°33′W	9840	10.3.	15.05	HYDR + PCS	rocks or stones	7550–10100	–	–	0	912	–	PCS empty
686	Tonga Trench	20°53′S 173°31′W	9770	11.3.	7.35	HYDR + PCS	grey clay	7860–10390	–	–	0	445	–	PCS: 90 cm.
689	Tonga-Samoa	13°03′S 170°46′W	4980	15.3.	18.00	HYDR + KCS	brown clay	4060–5210	–	–	0	230	–	KCS: 70 cm.
710	Off Mexico	19°42′N 105°41′W	670	26.4.	20.40	TOT+DR	350-500 m.	1500	–	20°	–	100	–	–
712	Off Mexico	17°00′N 102°42′W	4830–4730	28.4.	17.00	ST 600	–	6500	62°	58–60°	1.5	90	2.3	gear not at bottom
716	Acapulco-Panama	9°23′N 89°32′W	3570	6.5.	11.45	HOT	dark, muddish clay	8000	41°	41–43°	2.3	55	2.2	–
723	Gulf of Panama	5°38′N 79°30′W	3230	12.5.	11.00	PGI 0,2	dark clay	3600	–	–	0	–	–	41 1.
724	Gulf of Panama	5°44′N 79°20′W	2950–3190	12.5	18.40	ST 600	dark clay and stones	5500	40–48°	49–58°	1.8	120	3.6	bags torn
725	Gulf of Panama	5°43′N 79°20′W	2730	13.5.	0.20	PGI 0,2	–	3000	–	–	0	–	–	not released, gear entangled in wire
726	Gulf of Panama	5°49′N 78°52′W	3670–3270	13.5.	11.10	HOT	clay	8000	43°	43–47°	2.2	80	3	–

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727	Gulf of Panama	6°23′N 78°43′W	3570	13.5.	20.10	TOT + DR	850-1150 m.	3000	–	25–31°	2.5	170	7	–
728	Gulf of Panama	7°26′N 79°31′W	775	14.5.	11.00	LLH & LLS	–	–	–	–	0	540	–	200 hooks; line lost
	Gulf of Panama	7°26′N 79°31′W	775	14.5.	12.50	PGI 0,2	–	860	–	–	0	–	–	not released
	Gulf of Panama	7°26′N 79°31′W	755	14.5.	13.30	PGI 0,2	green clay	785	–	–	0	–	–	24 l.
729	Gulf of Panama	7°22′N 79°33′W	875	14.5.	14.55	PGI 0,2	green clay	905	–	–	0	–	–	29 l.
730	Gulf of Panama	7°21′N 79°32′W	995	14.5.	15.55	PGI 0,2	green clay	1015	–	–	0	–	–	39 l.
731	Gulf of Panama	7°20′N 79°33′W	1175	14.5.	17.20	PGI 0,2	green clay	1270	–	–	0	–	–	30 l.
732	Gulf of Panama	7°20′N 79°33′W	995	14.5.	18.25	PGI 0,2	green clay	1025	–	–	0	–	–	25 l.
733	Gulf of Panama	7°21′N 79°35′W	730–760	14.5.	21.30	LLH	–	–	–	–	0	720	–	200 hooks; no catch
734	Gulf of Panama	7°20′N 79°38′W	520	15.5.	1.25	PGI 0,2	green clay	525	–	–	0	–	–	24 l.
735	Gulf of Panama	7°23′N 79°38′W	400	15.5.	2.35	PGI 0,2	green sandy clay	424	–	–	0	–	–	21 l.
736	Gulf of Panama	7°20′N 79°36′W	600	15.5.	3.35	PGI 0,2	green clay	610	–	–	0	–	–	22 l.
737	Gulf of Panama	7°20′N 79°35′W	695	15.5.	4.20	PGI 0,2	green clay	700	–	–	0	–	–	not quantitative
	Gulf of Panama	7°20′N 79°35′W	695	15.5.	4.55	PGI 0,2	green clay	700	–	–	0	–	–	26 l.
738	Gulf of Panama	7°19′N 79°36′W	775	15.5.	5.55	PGI 0,2	green clay	800	–	–	0	–	–	25 l.
739	Gulf of Panama	7°22′N 79°32′W	915–975	15.5.	13.15	HOT	green clay	3800	25°	26–27°	2.5	60	2.5	–
740	Gulf of Panama	7°24′N 79°38′W	450	15.5.	22.00	LLH & LLS	–	–	–	–	0	960	–	200 hooks; no catch
741	Gulf of Panama	7°28′N 79°36′W	440–460	16.5.	0.05	ST 300 + D 45 + D 80	green clay	1500	–	–	–	60	–	–
	Gulf of Panama	7°28′N 79°36′W	520	16.5.	2.40	PGI 0,2	green clay	525	–	–	0	–	–	40 l.
742	Gulf of Panama	7°28′N 79°37′W	500	16.5.	3.20	PGI 0,2	green clay	515	–	–	0	–	–	30 l.
743	Gulf of Panama	7°27′N 79°37′W	600	16.5.	4.40	PGI 0,2	green clay	620	–	–	0	–	–	17 l.
744	Gulf of Panama	7°28′N 79°39′W	420	16.5.	6.10	PGI 0,2	green sandy clay	450	–	–	0	–	–	25 l.

Station	Locality	Position	Depth in metres	Year Date	Hour	Gear	Bottom or estimated fishing depth (E. F. D.)	Wire out metres	Inclination of wire		Speed in knots	Duration of haul in minutes	Length of haul in sea-miles	Remarks
745	Gulf of Panama	7°15′N 79°25′W	915	16.5.	17.05	ST 600 + D 45 + D 80	green clay	3000	–	–	–	**40**	–	–
746	Gulf of Panama	6°42′N 80°18′W	3470	17.5.	5.40	HOT	–	8100	40°	40–49°	2.4	45	–	gear totally lost
747	Gulf of Panama	6°39′N 80°32′W	3490	17.5.	11.25	HYDR + KCS + DR	–	0–3675	–	–	–	290	–	KCS: 105 cm.
748	Gulf of Panama	6°35′N 80°48′W	3420–3460	17.5.	23.20	HOT	–	6800	43°	43–45°	2	65	2	ship stopped for 4 hours, gear totally lost
758	Puerto Rico Trench	18°45′N 66°27′W	2840	30.5.	23.30	ST 600	–	5000	46°	50–57°	1.5	60	1.5	One bag lost, one torn
759	Puerto Rico Trench	18°30′N 66°15′W	1250	31.5.	6.15	PGI 0,2	stiff red clay	1300	–	–	–	–	–	19 l.
761	Sargasso Sea	25°00′N 56°02′W	6300	4.6.	8.40	SOT	–	11200	50°	50–55°	2	120	–	gear and 3500 m. wire lost
771	Gulf of Biscay	47°48′N 8°26′W	1920	18.6.	11.10	PGI 0,2	stiff clay	2000	–	–	0	–	–	17 l.
772	Gulf of Biscay	48°00′N 8°18′W	1520	18.6.	13.10	PGI 0,2	–	1700	–	–	0	–	–	released before reaching bottom
	Gulf of Biscay	48°00′N 8°18′W	1520	18.6.	14.40	PGI 0,2	–	1800	–	–	0	–	–	a few cc.
773	Gulf of Biscay	47°50′N 8°23′W	1680	18.6.	18.10	PGI 0,2	sand and dark clay	1900	–	–	0	–	–	50 cc.
774	Gulf of Biscay	47°52′N 8°23′W	855	18.6.	20.10	PGI 0,2	–	1000	–	–	0	–	–	a few cc.

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PRIMARY OCEANIC PRODUCTION

THE AUTOTROPHIC PRODUCTION OF ORGANIC MATTER IN THE OCEANS

By E. STEEMANN NIELSEN *and* E. AABYE JENSEN
Copenhagen Vejle

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PREFACE

During the summer of 1949 the final plans were settled for sending a Danish naval ship round the world. Oceanographic investigations were to be the main task of the expedition. The senior author who had started his work as a planktonologist during another Danish expedition round the world by the "Dana" 1928-1930 was excited by the idea of attempting to measure the organic productivity in the sea. No method for such a determination was, however, available. The only method tried before in the ocean had given results which seemed to be in absolute disagreement both with measurements of the standing crop of phytoplankton in the ocean and with theoretical considerations concerning the background of oceanic productivity.

A new method therefore had to be developed. We were very fortunate in having just received in Denmark the first quantity of radiocarbon – ^{14}C. The availability of this tracer made it possible to develop a new technique. Although the time was rather short for such a work, there was no choice.

As neither of the present authors had worked with tracers before the successful development of the technique was greatly assisted by the help and instructions given by dr. Hilde Levi of the Zoophysiological Laboratory, University of Copenhagen.

Both authors took part in the expedition during the first three months after which the senior author returned home. Most of the field work has thus been done by the junior author. The phosphate determinations were made by Mr. I. Crossland, M. Sc. and Mr. U. Kläning, M. Sc.

Part I is written by the two authors together, Part 2 and 3 by the senior author.

We are greatly obliged to the Committee of the Expedition and the Royal Danish Navy for facilities on board. We offer our sincere thanks to A. F. Bruun, Ph. D., leader of the Expedition. Dr. Bruun had the most ungrateful job of administrating the available time, which was always too short. His keen interest in the work on productivity was a great help. Thanks are also due to the commanders of the "Galathea", during the first part of the Expedition, Kommandørkaptajn H. Madsen and later Kommandør S. Greve, and to all others on board the ship.

INTRODUCTION

Phytoplankton production is the biological basis of all life in the oceans. This was recognized early by oceanographers. The investigation of oceanic plankton in respect to quantity was started at the end of the last century. Most of the important pioneer work was done by Germans. First of all must be mentioned the "Plankton Expedition" 1899. Hensen, the leader of the expedition, published (1911) in the concluding volume of the publications from the expedition a comprehensive treatise of the problems concerning oceanic productivity. The results were, however, in this respect not very satisfactory. The methods available for quantitatively estimating phytoplankton at the time of the expedition were rather inadequate, particularly for work in oceanic water. Silk nets were used.

Another German, Lohmann, must be recognized as the real father of oceanic quantitative phytoplankton science. During the "Deutschland" Expedition 1911 he used a method worked out by him at Kiel, whereby samples of water obtained from series of depths were centrifuged and the organisms counted in a living state. This method, although encumbered with systematic errors – cf. p. 115 – may still be recognized as one of the best for estimating the quantity of oceanic phytoplankton.

The route of the "Deutschland" Expedition covered representative parts of the subtropical and tropical parts of the North- and South-Atlantic. The general conclusions by Lohmann 1920 about productivity in these waters must still be considered valid.

The work by Lohmann was continued by Hentschel during the "Meteor" Expedition, 1925-27. This expedition covered the whole of the South-Atlantic down into the Antarctic Ocean and parts of the North-Atlantic. The phytoplankton population was determined at more than 300 stations rather regularly scattered over the whole area in question.

The results which were published by Hentschel 1932-1936 are in perfect agreement with Lohmann's work and because of the multitude of stations, give a still more instructive picture of the quantitative distribution of phytoplankton in an ocean. It is amazing to recognize how regular and simple is the quantitative distribution of plankton algae in the oceans.

The standing crop of plankton was measured according to Lohmann's method. It is often pointed out, e.g. by Harvey 1945 p. 142, that the evaluation of such counts can be interpreted only by an expert familar with the various species as they occur in the area in question. This view cannot, however, entirely be approved regarding the oceans. The variation in the cell size of the important phytoplankton organisms occuring in the open sea seems to be fairly constant from area to area. Further, it is rather moderate. The sum of the individuals of all organisms occuring gives a rather instructive picture of the quantity found, as convincingly shown, by both Lohmann and Hentschel. The pessimistic view on plankton counts seems to have been put forward by people acquainted primarily with coastal phytoplankton organisms taken with nets. The variation in size may here indeed be very great. It must, however, be pointed out that even in coastal waters the giants among the plankton algae only on rare occasions are of decisively quantitative importance provided that an artificial selection due to the net has not taken place. Furthermore the giants among the diatoms are not so important, most of the cell volume in these species being cell sap in contrast to the small sized species. When evaluating plankton counts from coastal waters it is mandatory to take the size of the algae into account. It is of course also necessary to estimate the different cell sizes when dealing with oceanic phytoplankton – see p. 115.

A measure of the standing crop of phytoplankton has been obtained by dissolving the plant pigments in acetone or alcohol and estimating either the mixed pigments or the chlorophyll. Kreps and Vejrbinskaya, 1930, were the first to use such a method. Net catches were originally used for these measurements. An important improvement was introduced by filtering a definite volume of the sea water from the different depths through paper (Riley 1939) or better through a Cella-Filter (Krey 1939). Much faith in this method has been shown from nearly all sides. Recently, however, some doubts about the general reliability have arisen (Gilbricht 1952) as it has been shown that a material part of the chlorophyll found sometimes may have nothing to do with living algae.

It is of great importance to know the size of the standing crop of plankton. It is, however, at least as important to obtain information about the daily production of organic matter by the plankton algae. Without such information it is impossible to estimate the food available for the animals. The word "production" is unfortunately used by different authors in very diverging senses. In this treatise we therefore use instead the more precise designation: primary "production of organic matter", which includes only autotrophic production due to photosynthesis and chemosynthesis. In coastal waters some investigations, although not too many, were made in the years after 1920 when Atkins 1923 using indirect methods and Gaarder and Gran 1927 using an experimental method started such work (for references see: Steemann Nielsen 1952). In the open ocean indirect methods of measuring the organic production are only possible at higher latitudes, where an unproductive winter season and a productive summer season alternate. Bogoyavlenskii (1955) has used such methods in the most northern part of the Pacific. In oceanic waters of lower latitudes only investigations made by Riley (1939) can be mentioned. As pointed out by Steemann Nielsen 1952, 1954, 1955 the results of these investigations (Gaarder and Gran's technique) can hardly be considered realistic. It seems to be the reduction of the bacterial activity in the illuminated experimental bottles which was measured instead of the photosynthesis of the plankton algae. This reduction seems to be caused by antibiotics produced by the algae in the light; cf. the 1955 article.

For measuring oceanic productivity a much more sensitive method than the light-and -dark bottle oxygen method introduced in marine biology by Gaarder and Gran has to be employed. The availability of the radioactive tracer ^{14}C after the last war made it possible to develop the technique to be described in Part I.

PART I. THE METHODS

A. GENERAL INFORMATION ABOUT THE ^{14}C-METHOD FOR MEASURING ORGANIC PRODUCTIVITY IN THE SEA

The ^{14}C-technique used on the "Galathea" Expedition has already been described by STEEMANN NIELSEN 1952. The main lines will, however, be reviewed here. Further, some important additional information will be given and the importance of some of the details, which may seem unimportant to some without further discussion, will be stressed.

In the ^{14}C method the incorporation of the tracer in the organic matter of the plankton algae is used as a measure of the production. A definite amount of $^{14}CO_2$ is added to the sea water the productivity of which is to be measured. The content of CO_2 (total) in this water must be determined or estimated (see p. 54). If we assume that $^{14}CO_2$ is assimilated by the plankton algae only through photosynthesis (see, however, p. 55) and that $^{14}CO_2$ is assimilated photosynthetically at the same rate as $^{12}CO_2$ (cp. p. 56), by determining the content of ^{14}C in the plankton after the experiment, we also determine the total amount of carbon assimilated. It is only necessary to multiply the amount of ^{14}C found by a factor corresponding to the ratio between CO_2 (total) and $^{14}CO_2$ in the water at the begining of the experiment. The amount of ^{14}C assimilated is determined by measuring the β-radiation from the plankton, which is retained by a collodion filter.

As ^{14}C has a half life of more than 5.000 years, samples with a definite content of $^{14}CO_2$ could be prepared before the start of the expedition. 1 ml. samples of water were used which had nearly the same content of total CO_2 as normal sea water. The water had a content of NaCl a little lower than oceanic seawater; the pH was 9.5. The ^{14}C-samples were kept in sealed glass containers (ampoules – Fig. 1). They were autoclaved at once after the preparation, as otherwise the possibility of bacterial growth and associated dark fixation of the tracer may cause trouble. The water used for preparing the $^{14}CO_2$ solution has to be distilled immediately before the use as otherwise the bacteria count may be too high.

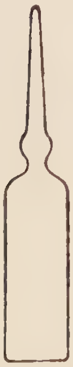

Fig. 1. Ampoule.

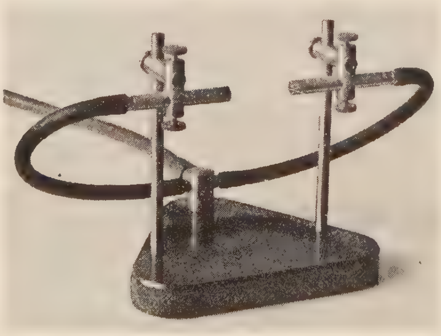

Fig. 2. Burner for sealing of ampoules (after JERMSTAD and SCHOU).

As the small ampoules are extremely difficult to clean on account of their narrow necks, previously sealed ampoules of jenafiolax glass were used. These were not only absolutely clean inside but were sterile, due to sealing during their manufacture. The ampoules were opened just before being filled. Presealed ampoules seem only to be manufactured and sold in Europe.

Whereas the filling of the ampoules may be done appropriately without difficulty the subsequent sealing may prove difficult. A special burner for this process – Fig. 2 – was used for the preparation of the glass containers for the "Galathea"-Expedition. It is to be recommended for workers not especially acquainted with pharmaceutical technique to autoclave the filled and sealed glass containers in a solution of methylene blue (0.1 %). On cooling, the blue solution is sucked into any glass containers which have not been effectively sealed. These are thus easily recognizable.

The $^{14}CO_2$ solution in the ampoules must have no contamination of any kind. If any contamination was found at all in the "Galathea" ampoules it was minimal, in maximum 5 per cent. of the background.

According to a statement by RYTHER and VACARRO 1954, 1 ml of their solution had a rather variable contamination of radioactive particulate material averaging 200 per cent. of the background. They stated therefore that the lower limit of sensitivity of the ^{14}C method was 1.3 mg C/m^3. During the "Galathea" Expedition photosynthetic rates as low as 0.1 mg C/m^3 could be measured to $\pm$ 10 per cent. If it had been necessary, still smaller rates could have been measured. According to a personal communication, Ryther and Vacarro are now able to prepare the tracer stock solution without contamination.

^{14}C was supplied from Oak Ridge, U.S.A., in the form of $BaCO_3$ with 4.79 per cent. of the carbon in the form of ^{14}C. As $BaCO_3$ is insoluble the CO_2 was converted into Na_2CO_3 as follows.

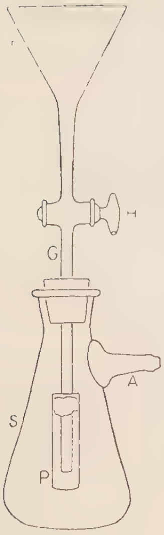

Fig. 3.
Vacuum line.

A specially constructed vacuum line was used (Fig. 3). A glass tube (G) carrying a funnel (T) and stopcock (H) is inserted in a pyrex glass suction flask (S) through the rubber stopper. A glass vessel (P) is attached to tube (G) by means of a cottonwool plug and a wire. $Ba^{14}CO_3$ and a suitable amount of normal $BaCO_3$ to act as a carrier is placed in the vessel (P). A solution of NaOH (generally 5 ml. 0.5 N) is placed at the bottom of the suction flask. Then HCl (generally 5 ml. 0.5 N) is poured into the funnel. After evacuation the suction flask is closed by a cock immediately outside the side tube (A). The cock (H) is now opened cautiously and the hydrochloric acid is run into vessel (P). This releases CO_2 which diffuses down to the NaOH solution, and is absorbed by it.

During the effervescence in vessel (P), some of the liquid will be thrown on to the cotton-wool, which must eventually be completely steeped in the hydrochloric acid in vessel (P) in order to ensure that the carbon dioxide in the barium carbonate which may have been thrown on to the cotton-wool is released. If the original quantity of hydrochloric acid is not sufficient, a little distilled water is added through the funnel (T).

Although experiments have indicated that essentially all the carbon dioxide in the barium carbonate is absorbed in the sodium hydroxide solution after 15 minutes, the apparatus is left to stand for a further 60 minutes. It is then opened and the stopper, together with tubes (P) and (G), funnel (T) and cock (H), removed. Then 200 ml. glass-distilled water is added; after shaking, 10 ml. is removed and titrated electrometrically with hydrochloric acid to pH 9.5. A corresponding amount of hydrochloric acid is added to the remaining 195 ml. and the 10 ml. are poured back. After checking that the pH is actually 9.5, a solid rubber stopper is placed in the mouth of the suction flask and the liquid is transferred to 1 ml. glass containers (Fig. 1) by means of a graduated (automatic) syringe. The liquid is withdrawn through the side tube (A) of the suction flask after the latter has been turned upside down. The glass containers are then sealed. The relatively high pH (9.5) prevents any appreciable loss of activity during the various manipulations. That this is really so appears from the fact that it is impossible to demonstrate any progressive reduction in activity from the glass container first filled to that last filled. In the subsequent addition of the contents of the ampoules to the water samples in which the photosynthetic activity is to be measured, it is also important that pH should be comparatively high.

For the "Galathea" Expedition 1 ml. ampoules of 4 different strengths were prepared. The different containers were made in series of 200, and were each wrapped in appropriately coloured tissue paper. Within series of the same calculated strength the correspondence was fairly close. In later calculations values for the particular series were always used. The series of the greatest strength contained 8 μC per ampoule, the series of the weakest strength, 0.2 μC.

For counting carbon dioxide was precipated as barium carbonate, which was then filtered off by the usual collodion filter or a smooth paper filter (3 sq. cm., see p. 54). Carrier was also added, and the weight per 3 sq. cm. was always about 20 mg.

In later work millipore-filters (Lowel Co, U.S.A.) have been used for measuring the activity of an ampoule instead of the ordinary collodion filters. These filters do not change weight if an aqueous solution is passed through. Regarding the determination of a self-absorption curve the reader is referred to CALVIN *et al.*, 1949 p. 31 and p. 104 f.f.; such a curve is presented in Fig. 4. By using Geiger tubes with windows of the same mass thickness identical curves were obtained. Some technical skill is necessary to make an adequate self-absorption curve.

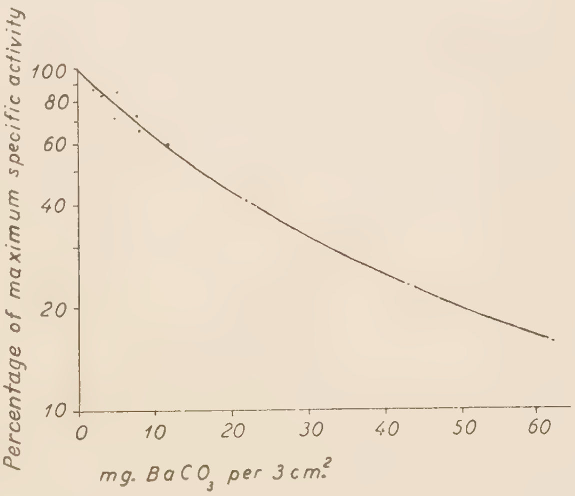

Fig. 4. Self-absorption correction curve.

B. THE DETERMINATION OF THE PHOTOSYNTHETIC ACTIVITY OF PLANKTON ALGAE

After the content of a ^{14}C ampoule has been added to a water sample containing plankton algae and the sample then has been exposed to light, part of ^{14}C is found in the organic matter of the plankton algae. If this quantity of ^{14}C is to be used as a measure of the photosynthetic intensity, we must know both the content of total CO_2 in the water and the ratio $\frac{^{12}C + ^{13}C + ^{14}C}{^{14}C}$ in the total CO_2 of the water. As a rule, however, we shall avoid using absolute amounts of ^{14}C, as only the activity of the experimental water and the activity of the plankton algae are to be determined. If, under identical conditions the activity of the experimental water is a, that of the plankton algae b, and the content of total CO_2 in the water c, then the total amount of CO_2 assimilated by the algae is $\frac{b \times c.}{a}$ This is on the assumption that $^{14}CO_2$ is assimilated at the same rate as $^{12}CO_2$ and that ^{14}C is not incorporated in the algae in any other way than through photosynthesis. In Section C this question will be discussed in detail.

If pH, titration alkalinity, and temperature are known, it is possible, according to BUCH (1945), to determine total CO_2 in fresh water provided that the titration alkalinity does not approach zero. In sea water it is also necessary to know the chloride content, which has partly a direct effect, partly an indirect effect through the boric acid, the concentration of which is proportional to the chloride concentration. In oceanic water the calculation of total CO_2 thus becomes slightly more complicated than in fresh water (see HARVEY 1945, pp. 52-73).

If Cl‰ is known, it is not necessary to determine the titration alkalinity A, as this is equal to 0.000123 Cl‰ expressed in equiv./l. With brackish water, as with fresh water, it is necessary to determine the titration alkalinity.

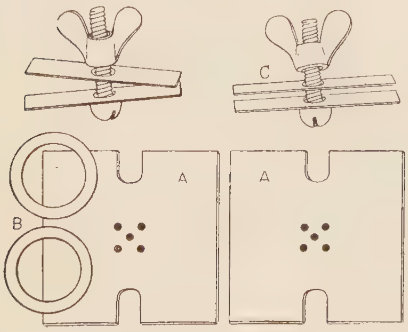

Fig. 5.
Special holder for collodion filters.

As pH varies so little in oceanic surface water, it is unnecessary to determine pH unless very high accuracy is aimed at. If it is put at 8.20, the error in total CO_2 will be 2 to 3 per cent. at the most. Normally for the present purposes it will be sufficient to put total CO_2 at 90 mg/l. for normal oceanic surface water.

The β ray activity of the plankton algae was measured after filtration through a collodion filter (membrane filter from Membranfiltergesellschaft, Göttingen). These filters are kept dry before use; this is a great advantage as compared with the prewar collodion filters, which had to be kept in water. Filtering was done by suction (in the "Galathea" a mechanical pump was used). The filtering surface was 3 sq. cm. Facilities for automatic filling were provided. The filtration device corresponds to that in CALVIN et al., 1949 fig. 40. In the "Galathea" 6 sets of this apparatus were placed so that they could all work at the same time. The filters used resemble closely the standard filter "mittel" of the factory. 300 ml. distilled water take about 20 minutes to pass through the filter. A considerable quantity of plankton reduces the rate materially; in these circumstances part of the sample is filtered. The maximum size of the pores is 0.5 μ. All marine autrophic plankton algae are retained. With most – perhaps all – waters it is possible to use filters with a slightly greater pore width (at most about 0.8 μ), so that it is possible to increase the rate of filtration materially.[1]

When filtration was completed, about 5 ml. of sea water free from activity was added for rinsing, etc. The filters were then placed in a special holder (fig. 5), dried in air for about 12 hours, and placed for 20 minutes in a closed container above fuming hydrochloric acid. This was done in order to remove carbonate to be found e.g. in coccoliths. Experiments have shown that all carbon in inorganic form is removed in this length of time, so that only ^{14}C in organic form, which is not destroyed by the process, is left. Immediately afterwards the filters must be dried in a desiccator – also containing some soda lime – and if they are not examined at once, kept there. If this is not done, the plankton sometimes may absorb water because calcium chloride is developed. Water containing organic matter with dissolved ^{14}C may thus be sucked into the filter. Before the filter is finally dried, it is placed on a special mounting ring and base (CALVIN et al., 1949, fig. 41).

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[1] The firm has recently renamed their filters. We are now using filters "grob", Stufe 2.

An end-window Geiger-Müller counter tube with a window radius of 7.5 mm. (made by Zerahn and Madsen, Copenhagen) proved most suitable for measurement of the radio-activity. For the "Galathea", Geiger tubes with a particularly thin window were selected. Care must be taken that the activity of a sample is about 10 times larger than the background.

A double counting unit made by Brüel and Kjær, Nærum, Denmark, was used. It has proved robust in all kinds of climate. The technicians of the Expedition were able to correct all faults that developed in the unit. A special 220- volt generator, unconnected to other circuits, supplied the current in the "Galathea".

As the geometry used in measuring the barium carbonate for determing the activity of the contents of the ampoules is identical with the geometry used in measuring the activity of the plankton, the two activities may be directly compared. As the weight of plankton was always below 0.1 mg. per 3 sq. cm. self absorption in the plankton may be disregarded.

At the start of an experiment, the contents of an ampoule are added, by means of an ordinary hypodermic syringe or a glass pipette, to the bottle with the sample in which the photosynthesis is to be measured. The container is rinsed with a little water from the sample.

A sample of elementary carbon containing ^{14}C, mounted on the same mounting ring and base as normal samples with the same area was always used as a standard.

C. IS THE AMOUNT OF ORGANICALLY BOUND ^{14}C A MEASURE OF THE INTENSITY OF PHOTOSYNTHESIS?

If the amount of organically bound ^{14}C in the plankton after an experiment is to give an absolute measure of the intensity of photosynthesis (the gross production) the following conditions must be present: – (1) No $^{14}CO_2$ must be incorporated in organic compounds except through photosynthesis, (2) the rate of assimilation of $^{14}CO_2$ must be the same as that of $^{12}CO_2$, (3) no $^{14}CO_2$ must be lost by the respiration which takes place simultaneoulsy with photosynthesis, (4) no organic matter must be lost by excretion.

None of these conditions are, however, quite fulfilled. Although the importance of each of them is only relatively slight at high light intensities and one of them has the opposite effect to the others it is necessary to introduce a correction (valid at high light intensities) covering them all.

As it is now generally known, both animals and plants have a dark interchange of CO_2 which has nothing to do with photosynthesis. Labelled CO_2 is in this way introduced into organic matter of both plants and animals. In a healthy culture of a plankton alga such a dark fixation of $^{14}CO_2$ is negligible compared with the fixation due to photosynthesis at a high light intensity as shown by BROWN, FAGER and GAFFRON 1949 and many others. In fig. 6 is presented the dependence of the length of the experimental time on the rate of dark fixation of $^{14}CO_2$ as given in per cent. of the photosynthetic fixation at optimum light intensity. *Chlorella pyrenoidosa* was used for these experiments. Compared with the fixation of $^{14}CO_2$ in the light the dark fixation was particularly low in the experiment presented in Fig. 6. The concentration of total CO_2 was much lower than in seawater. In experiments lasting four hours the dark fixation in water from the photic layer in the sea is mostly about 1-2 per cent. of the fixation at optimal light intensity. It may sometimes be as

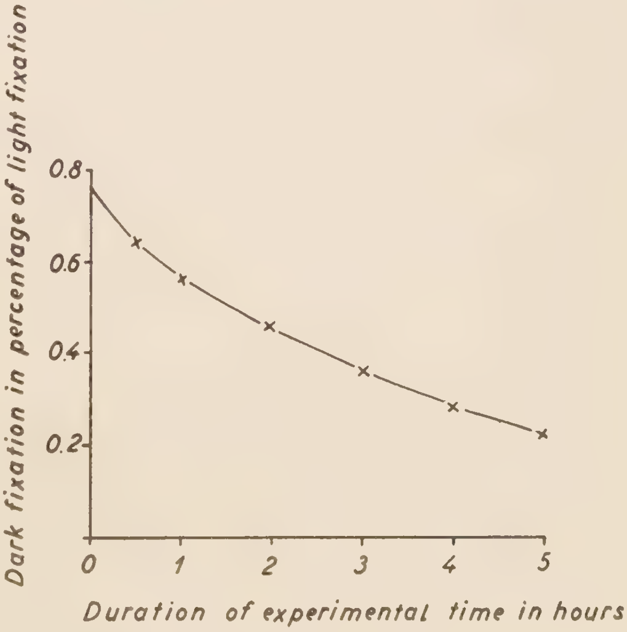

Fig. 6. Dark fixation of ^{14}C in percentage of fixation in light. *Chlorella pyrenoidosa.*

high as 5 per cent. even in oceanic water. It must be remembered that the dark fixation by other organisms than the algae is included.

It was impossible during the "Galathea-Expedition" to make determinations of the dark fixation in all the water samples in which the rate of photosynthesis was determined. It was only done in part of them. The stock of the ampoules of the greatest activity was too small. The ampoules used for a normal determination of photosynthesis did not give the sufficient accuracy when used for measuring dark fixation, the rate of which was only a few per cent. of the rate of the fixation in light.

In more recent Danish investigations dark fixation has been measured in all water samples. For special investigations this is of importance. For normal measurements of the rate of photosynthesis it is unnecessary. If the autotrophic algae constitute only a minor part of the bio-mass present in the sea or if the photosynthetic rate is very low due to e.g. lack of light, dark fixation may be a more dominant part of the total fixation of $^{14}CO_2$. In polluted waters where huge quantities of bacteria are found, dark fixation may be of extraordinary importance. In the oceans it seems, however, never to be so if only a relatively high light intensity is employed and the experiments only have a duration of some few hours.

In agreement with Anderson and Libby 1951, it was theoretically estimated by STEEMANN NIELSEN 1952 that $^{14}CO_2$ should be photosynthesized 6 per cent. slower than $^{12}CO_2$. A recalculation of some experimental results obtained by van NORMAN and BROWN 1952 has shown that $^{14}CO_2$ is really assimilated about 5 per cent. slower than $^{12}CO_2$ (STEEMANN NIELSEN 1955). It was necessary to recalculate van NORMAN and BROWN's figure as, inter alia, they have paid no attention to the fact that about 50-70 per cent. of the CO_2 produced – or expected to be produced – by the respiration in some way or other is identical with CO_2 fixed during photosynthesis – STEEMANN NIELSEN 1955.

If it is assumed that the rate of respiration is about 10 per cent. of the photosynthetic rate at a high light intensity – cp. below – the interaction of respiration and photosynthesis will have the effect that the photosynthetic rate as measured by the ^{14}C method is about 6 per cent. too low. This correction was put at 4 per cent. by STEEMANN NIELSEN 1952.

If these three corrections are added together we get a total correction of $(+5+6-1) = +10$ per cent. The same total correction was used during the preliminary working up of some of the "Galathea" material (STEEMANN NIELSEN 1952).

The correction + 10 per cent. is only valid if the rate of photosynthesis is high as compared with the rate of respiration. If the rate of respiration is 5 % of the rate of photosynthesis, the correction should only be 7 %. If on the other hand the rate of respiration is 25 %, 50 %, or 100 % of the rate of photosynthesis, the correction should be about + 20 %, + 50 %, and + 155 % respectively. This means that measurements made with the C-14 technique at the compensation point would have to be multiplied with a factor of about 2.5 to obtain values for gross production. Therefore, it must be stated that the C-14 technique is only applicable with reservations if the rate of photosynthesis is not considerably higher than the rate of respiration. During the "Galathea" Expedition the normal measurements were made at a high intensity – about 18.000 lux cf. p. 60. The 12 experimental series made during the Expedition showing the dependence of the rate of photosynthesis on light intensity – cf. p. 101 – indicate for all kinds of surface water, that the rate of photosynthesis at 18.000 lux is high as compared with the rate of respiration – about 10 times as high. It is impossible to state any difference in the shape of these curves between the plankton from eutrophic and oligotrophic waters – cf. Figs. 32-36.

According to recent investigations in the North Atlantic by STEEMANN NIELSEN and HANSEN (under preparation) the ratio of rate of respiration to rate of optimal photosynthesis normally is less than $^1/_{10}$ in oceanic subsurface water.

The "in situ" experiments – cf. p. 57 and p. 67 – were only made during daytime, thus decreasing the influence of respiration by the factor 2. Finally these measurements were not carried on right down to the supposed compensation depth. Special corrections were made for the measurements from the lowest part of the photosynthetic layer. It should, however, be mentioned that even considerable deviations in the photosynthetic rates in the lowest part of the photosynthetic layer only slightly influence the size of organic production per surface unit.

No correction is made for organic material excreted by the algae. In the light of the modern knowledge concerning algal physiology there is no reason to consider such an excretion as being of any real importance in experiments of short duration at normal light intensities – cf. MYERS and JOHNSTON 1949.

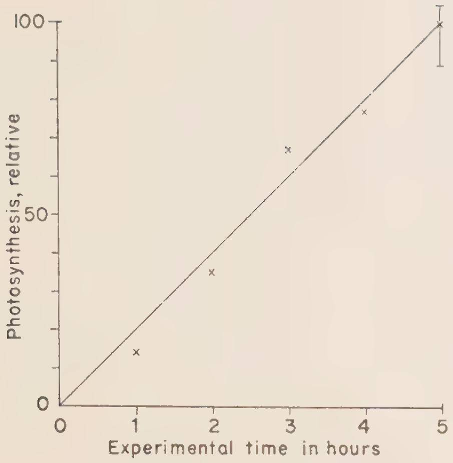

Fig. 6a. Dependence of the rate of photosynthesis on time. The variation is shown of five parallel experiments lasting 5 hours. St. 719a.

The duration of the normal experiments was 4 hours. The experimental series presented in Fig. 6a shows – like other similar series – that the rate of photosynthesis at a nearly optimum light intensity keeps constant at least during the first 5 hours. Surface plankton from the eastern part of the Pacific Ocean near Panama was employed illuminated at 18.000 lux. Identical water samples were illuminated for 1, 2, 3, 4, and 5 hours. 5 samples were illuminated for 5 hours. The rate of photosynthesis during the first hour was lower due to an after-effect of light inhibition - cf. p. 102.

It must always be considered wise to make the duration of experiments with natural plankton short. Firstly oceanic plankton algae are not able to stand the conditions in the experimental bottles for long periods – cf. p. 99. When using the ^{14}C-technique there is a special reason to keep the duration of the experiments short. If autolysis of the algae is taking place this technique gives very poor results as a material part of the organic matter containing the tracer will not be retained by the filter. Autolysis may easily take place due to photo-oxidation in experiments of long duration, particularly if there is no continuous stirring. As during the "Galathea" Expedition all experiments were of short duration and as effective stirring was employed, it is rather unlikely that autolysis played any serious rôle (see also p. 67). It is on the other hand likely that small amounts of water-soluble assimilates are lost during the filtration.[1]

The suppositions put forward by RYTHER 1955 regarding the use af the ^{14}C method in oligotrophic water are discussed by STEEMANN NIELSEN and AL KHOLY 1956. Furthermore, all evidence indicates that an absolute deficiency in P or in N is normally not found in nature – cf. p. 114.

It is possible that misleading results may be achieved in seawater with a very small concentration of plankton algae, if the duration of the ^{14}C-experiments is several days. The dark fixation of ^{14}C by the bacteria developing in huge quantities – cf. STEEMANN NIELSEN 1955b – may completely outdo the fixation due to photosynthesis.

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[1] According to a personal communication from dr. G. E. Fogg, London, fixation of radiocarbon in filter-passing organic material in water from a eutrophic lake has been found to be only about 1 per cent of that in material retained on the membrane filter.

D. THE "IN SITU" METHOD FOR DETERMINING THE PRODUCTION PER SURFACE UNIT OF THE SEA

For determining the production of matter under 1 sq. m. of surface, a method resembling Gaarder and Gran's oxygen method can be used. Instead of measuring oxygen metabolism, the intensity of photosynthesis is determined by the ^{14}C method.

With an all-glass water-bottle (fig. 7, for a description see AABYE JENSEN and STEEMANN NIELSEN, 1952) 500 ml. of water is taken from the various layers of water in which photosynthesis is believed to take place. This may be decided by measuring the penetration of light into the sea (see p. 63). After a 300-ml. bottle (pyrex, with glass stoppers) has been filled and the contents of a ^{14}C ampoule introduced, the bottle is lowered to the depth from which the sample came. This is done either immediately before sunrise or when the sun is at its meridian altitude. The bottle is raised again, either in the first case when the sun is at its meridian altitude, or in the second case immediately after sunset. In both cases, the photosynthesis measured relates to half a day, and the value found has only to be multiplied by 2 to relate to the whole day. To estimate the total photosynthesis below 1 sq. m. surface of the sea the determinations from the single depth are presented graphically as e.g. in Fig. 8. The area to the left of the curve drawn represents the photosynthesis below the surface.

The "in situ" method was little used during the

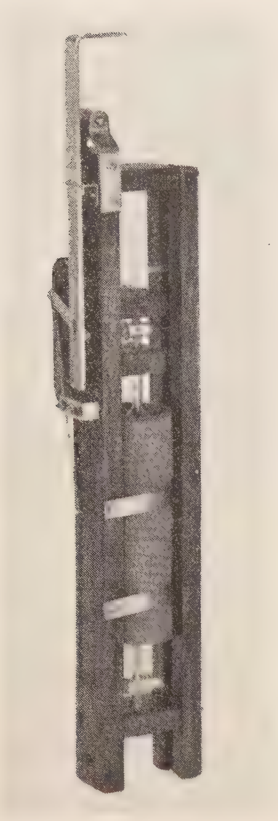

Fig. 7.
All-glass water-bottle.

“Galathea” Expedition. It is much too time consuming. It has, however, now been used regularly for some years both in Greenlandish and Danish waters. Light ships are particularly suitable for such studies. This work will be published elsewhere. Fig. 8 presents typical examples from all seasons from the Kattegat. The light conditions were in all cases favourable.

Five special “in situ” experimental series with surface water were made on the “Galathea” in order to investigate the dependence of the photosynthetic rate (real assimilation) on the light and to check the results obtained by the “tank” experiments. Four of these series are given in Fig. 9-12. All values are relative. The depth O = surface, the depth 100 is the depth at which an average of 1 per cent. of the green and blue light at the surface was found. The maximum rate of photosynthesis per day measured is put at 100 at the abscissa. The duration of the experiment was a half day – from noon to sunset. The curves would of course be identical if the duration of the experiments had been a whole day. It was bright weather during all series. The series shown in Figs. 9-11 were made in plankton-rich waters. The first mentioned was made with water from a depth of 10 m. off the coast of Angola – latitude 8°50′S – in December, the second was made in False Bay, South Africa – latitude 34°16′S – in January. Water from a depth of 4 m. was employed. The third series was carried out in the Gulf of Siam using water from a depth of 10 m. The depth showing 1 per cent. of the surface light (blue + green) was 43 m. in the first mentioned series, 18 m. in the second, and 60 m. in the third.

The experiment shown in Fig. 12, was made in clear oceanic water near Ceylon in the Indian Ocean. Water from a depth of 10 m. was used. The depth showing 1 per cent. of the surface light was 99 m.

As pointed out p. 56, the ^{14}C technique gives low values of the photosynthetic rate near the compensation point due to the intermixing of the respiratory and photosynthetic processes. The lower parts of the curves are corrected accordingly – dashed line. Dark fixation is not considered.

If the rate of respiration is put at 5-10 per cent. of the maximum rate of photosynthesis found, the compensation point during the day should be found at the dephts where 5-10 per cent. of the maximum photosynthetic rate is measured. The compensation point for 24 hours – a day and a night – is thus found at the depth at which 10-20 per cent. of the maximum

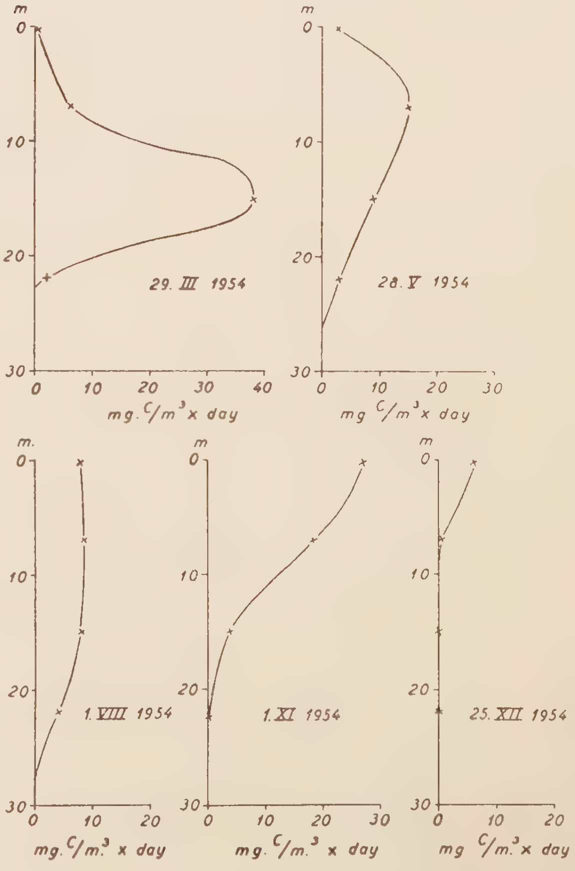

Fig. 8. Normal “in situ” experiments in the Kattegat.

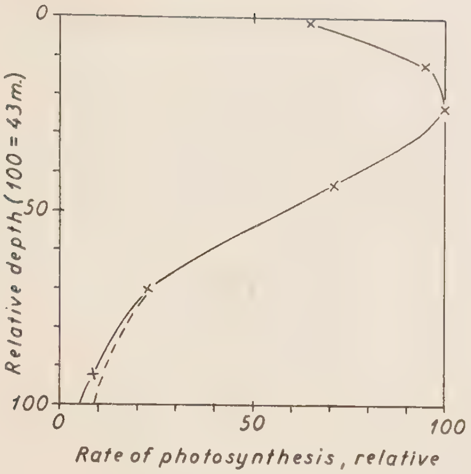

Fig. 9. Photosynthesis in water collected at 10 m. depth when exposed at different depths. St. 101.

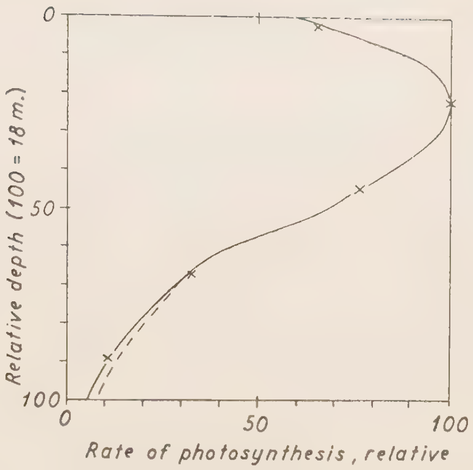

Fig. 10. Photosynthesis in water collected at 4 m. depth when exposed at different depths. St. 170.

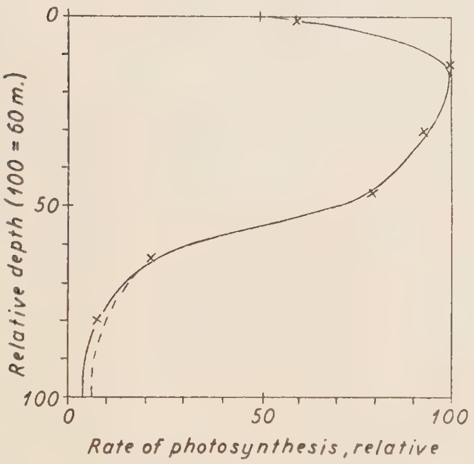

Fig. 11. Photosynthesis in water collected at 10 m. depth when exposed at different depths. St. 381.

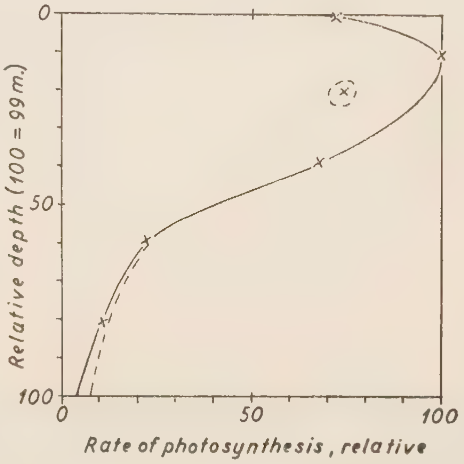

Fig. 12. Photosynthesis in water collected at 10 m. depth when exposed at different depths. St. 283.

photosynthetic rate is measured. As may be seen from Figs. 9-12 this depth corresponds approximately to the depth at which one per cent. of the surface light (blue + green) is found. Because of the intermixing of photosynthesis and respiration the compensation depth can only be presented with some reservation. This is, however, of only slight importance for the computation of the rate of photosynthesis per surface unit.

The areas to the left of the curves in Figs. 9-12 give the rate of photosynthesis below a surface unit. It is easily seen from all curves that this rate is practically identical with the rate at the "best depth" – the depth at which the highest photosynthetic rate is measured – multiplied with the depth at which 1 per cent. of the green + blue light is found, divided by 2. This formula is not only applicable in tropical and subtropical waters. It has also been shown with some modification to be valid in Danish waters (latitude 55°N) on bright days during summer – cp. STEEMANN NIELSEN 1951 Fig. 10. It is even possible to use the formula in arctic waters during summer as will be shown in a subsequent paper. The formula is the basis for computing the photosynthetic rate according to the "tank" method.

E. THE "TANK" METHOD FOR DETERMINING THE PRODUCTION PER SURFACE UNIT OF THE SEA

If only the "in situ" method could have been used during the "Galathea" Expedition only a few scattered observations on productivity could have been made. It is expensive to keep a big ship like the "Galathea" stationary for at least 6 hours – the duration of an "in situ" experiment in the Tropics. Furthermore, the program of the expedition was very extensive. The investigation of the organic productivity was only one of many topics of the expedition. A second, time-saving method for determining the production had therefore to be used.

With this method, water samples from the various depths, after addition of ^{14}C, are exposed to a definite light intensity in a water-bath at the same temperature as the sea. After 3 to 4 hours the plankton is filtered off and the photosynthetic intensity determined in the usual way. From the value of the photosynthetic intensity found for a given light intensity and temperature, the production of matter by photosynthesis through 24 hours can be calculated if we know firstly the dependence of photosynthesis on the light intensity, and secondly the light intensity at various times of the day at the depths from which the samples originate.

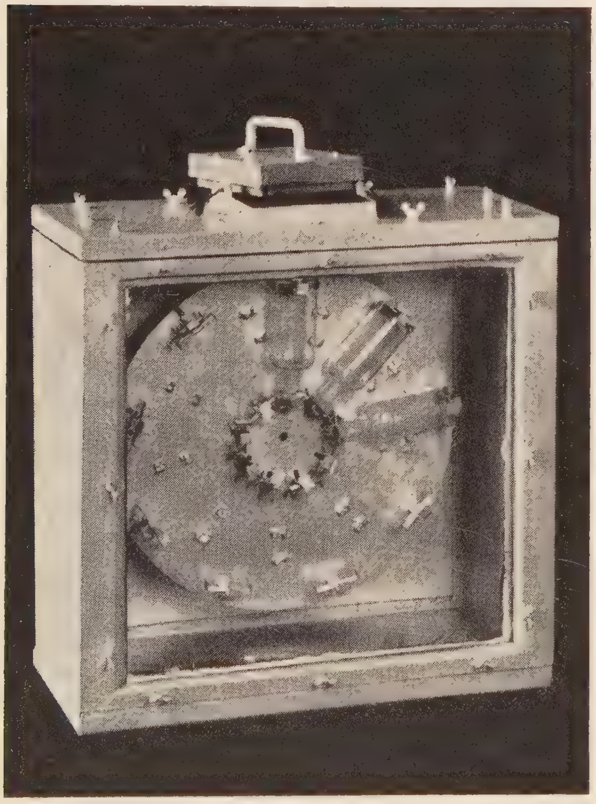

Fig. 13. Water-bath.

On account of the ship's movement at sea, the water-bath – Fig. 13 – is kept tightly closed. Through a trap-door in the middle of the top cover the bottles can easily be placed on the rotating disk in the middle of the bath, which can accomodate nine 300-ml. bottles. The spindle on which the disk rotates passes through the wall of the water-bath to a motor supplying the motive power. The whole front wall is glass, so that the experimental bottles can be illuminated by the twelve 20 W. tubular fluorescent lamps (Phillips 33a) which give a light with a spectral composition near that of the daylight. A mirror is placed behind the lamps. A ventilator was placed above the lamps.

Before the start of an experiment the temperature of the water in the water-bath is adjusted by adding ice, to about 1°C. below the temperature wanted. During a 4-hour experiment the temperature increases by 2°C. The increase in temperature is slight partly because the water-bath is very effectively insulated, and partly because tubular fluorescent lamps are used, which radiate very little heat. On the side of the water-bath facing the source of light partial insulation is provided by an extra pane of glass placed 1 cm. outside the pane in the bath.

All parts of the water-bath, including the rotating disk, are treated with silver-bronze, the light intensity thus being increased by about 50 per cent. With new fluorescent lamps the effective light intensity illuminating the water in the experimental bottles is about 20.000 international lux. This intensity, however, falls to about 18.000 lux in a comparatively short time. After a burning period of about 500 hours the light intensity is 14.000 lux: the lamp should be replaced before that stage is reached.

The idea behind the "tank" method is to expose the algae in the tank to a light intensity giving a photosynthetic rate identical with the average rate during a day in the sea at the "best" depth (Fig. 9). The production per surface unit may thus be found by multiplying the depth of the photosynthetic layer divided by 2. – according to the formula given on page 61.

Tank experiments made together with the "in situ" experiments given in Figs. 9-12 showed that the rate at the "best depth" during bright days was the same (about 90-110 per cent.) as in the tank if the light intensity which the algae received here was 18.000 int. lux.

The light intensity which the algae received in the tank could not be measured directly, as the algae received both the direct light and the reflected light particularly that from the rotating disk to which the experimental bottles were fastened. Instead the light intensity was measured indirectly. Light assimilation curves for surface plankton were produced using an open tank with the front window of glass for the higher light intensity. Facing this front window was placed an incandescent bulb able to produce sufficient high light intensities. The variation in light intensity in the open aquarium was produced by varying the distance of the experimental bottles from the bulb. The experiments at low light intensity were made in the normal tank without reflex light using filters to reduce the light intensity. The effective light intensity in normal tank experiments illuminated by the fluorescent lamps and with reflected light was put at the light intensity in the special experimental series giving the same photosynthetic rate as in the tank. In this way it could be stated that the reflected light in the tank increased the effective light intensity by about 50 per cent. At the same light intensity measured in the tank without reflected light, and in the special arrangement with incandescent light, the rate of photosynthesis was found to be practically identical. This was primarily caused by using overvoltage for the incandescent bulb- a special type designed for photographic use. Relatively much green and blue light was thus produced just as in the case of the fluorescent lamps. There is therefore no need for considering the different colour spectra of the two sources. The light intensities although measured in lux were only used relatively. The light-assimilation curves are discussed in detail in section III, C, 1.

If the light intensity in the tank measured without reflection was 12.000 lux and the effective light intensity thus 18.000 lux, no correction had to be made. If this was not the case, a correction to the measurements was made according to the curve shown in Fig. 14. The curve is drawn according to the experiments presented in section III, C, 1.

Samples from three different depths were collected, on a normal "Galathea" station: a) from the surface, b) from the depth at which the light intensity (blue + green) was 10 per cent. of the intensity at the surface, c) from the depth at which the intensity was 1 per cent.

If the temperature varied between the depths from which the three samples were collected, it was impossible to provide the right temperature for all samples. A correction for the photosynthetic rate therefore had to be made. The correction was put at 5 per cent. per degree Celsius. This correction was only of importance in some special areas.

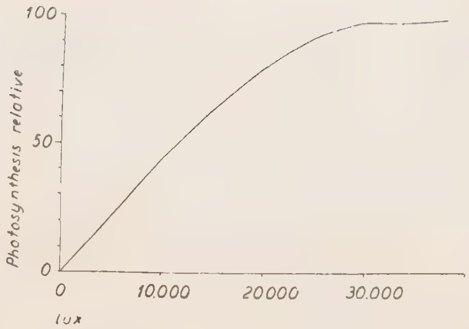

Fig. 14. Light intensity and rate of photosynthesis in tropical surface plankton.

The experiments shown in Figs. 9-12 in the previous section provided, as already mentioned, the necessary basis for deriving a formula for organic productivity.

Production of matter per sq.m. per 24 hours =

$$\frac{(2a + 2b + c) \cdot d \cdot e}{5 \cdot 2} \text{ mg.C}$$

where a is the photosynthesis in mg. C per hour per cu.m. at 18.000 lux in surface water;

b is that in water from a depth with 10 per cent. of the surface light;

c that in water from a depth with 1 per cent. of the surface light;

d is the depth in m. at which the light is 1 per cent. of the total quantity of blue and green light at the surface; and

e is the number of hours from sunrise to sunset.

The "in situ" experiments and the light-assimilation experiments have been made with plankton from surface water (0-10 m. depth) exclusively. In section III, C, 1 will be shown that the algae from the lower parts of the photosynthetic zone must be supposed to show a somewhat deviating dependence on light from that of surface algae. It will be shown, however, that the formula presented above may also to a first approximation be used for the algae from the lower depth.

As the photosynthesis taking place in the deepest layers of the photosynthetic zone is of less quantitative importance than that taking place in the upper and middle layer, the value for photosynthesis at 18.000 lux in the water from the depth with 1 per cent. of the light is entered in the formula at half its value.

The formula applies to the tropics and subtropics.

In higher latitudes the formula may be used approximately during summer, but not during the other seasons. If the phytoplankton is not too heterogeneously distributed vertically it appears to be possible to determine the production of matter per surface unit by the "tank" method with an accuracy of about ± 20 per cent. (perhaps a little less accurate during the first month of the expedition), which should normally be quite sufficient. Greater accuracy may be obtained by taking samples from other depths exceeding the three mentioned above. In waters where the algae are very heterogeneously distributed vertically an augmentation of the number of samples is desirable.

The production of matter in the sea depends of course on weather conditions, although to a lesser degree than would be expected at first sight. The dependence on weather is discussed in section III, C, 3. It must, however, be mentioned that all values calculated for the production per area are reduced by 10 per cent. The values directly obtained by the formula given above correspond to absolutely bright weather. If 10 per cent. is subtracted average values for "normal" weather are obtained.

F. THE ACCURACY OF THE PRESENT MEASUREMENTS OF THE PHOTOSYNTHETIC RATE IN WATER SAMPLES

By choosing glass containers with sufficient ^{14}C and counting for a sufficiently long time, it is possible to determine the assimilation of ^{14}C with very great precision. Normally the activity is determined to an accuracy of ± 5 per cent. To aim at a greater accuracy would serve no purpose.

The experiments described in table 1 were made to discover to what extent the intensity of photosynthesis varies in parallel samples.

A large volume of surface water from two tropical localities was thoroughly mixed and distributed among seven to eight 300-ml. bottles. The contents of identical ^{14}C ampoules were added to each bottle.

Table 1.

Surface water Banda Sea imp./min.	Surface water Flores Sea imp./min.
108	60
115	53
115	48
126	61
110	60
106	56
108	61
117	
M = 113 ± 2	M = 57 ± 2
σ (single determination) = 6.1	σ (single determination) = 4.5

After illumination at 18.000 lux for 5 hours, the contents were filtered and the activity of the plankton determined. The variation between samples is greater than the inaccuracy in measuring the activity.

In addition to the two series presented here a multitude of observations during the Expedition gave further evidence concerning the accuracy of the measurements. The 12 series made to show the light dependence of the rate of photosynthesis – see p. 101 – the 5 series made to show the dependence of the photosynthetic rate on depth – see p. 59 – the 4 series to show the influence of addition of nutrients – p. 99, all indicate that the variation between parallel samples is of the magnitude given in table 1.

All the single samples of one of the above series were portions of a large homogenous volume of water collected at the same time and stirred. If the single samples are collected in the sea separately, a conformity nearly as high would be expected at high sea, due to the plankton concentrations here being very homogeneous – Hentschel 1932-1936. In coastal waters a greater variation perhaps could be expected. Some investigations were made in the coastal waters of California. Table 2 presents the results.

Table 2. The variation in the rate of photosynthesis (relative) in surface samples, each collected at intervals of a few minutes.

	St. 705	St. 707	St. 708
A	110	90	97
B	89	79	102
C	102	133	102

The variations at the Stations 705 and 708 were of the same size as when portions of a single water sample are used. The variations were somewhat higher at St. 707.

G. MEASUREMENTS OF THE LIGHT PENETRATION INTO THE SEA

During the Swedish Deep-Sea Expedition 1947-48 on the "Albatross" very important studies on the submarine light in the oceans were made, JERLOV 1951, 1953, JERLOV and KOCZY 1951. The results reported on this subject previously were few.

Light measurements were made by the Swedish expedition only when the light conditions were absolutely favourable. In order to be able to present a physically indisputable picture of the light conditions in the oceans, measurements taken when conditions are not favourable must be rejected. Nevertheless it was possible to give a survey of the transparency in various ocean areas and to discuss the features of the horizontal and vertical variations of transparency. A relatively low penetration was observed in the upwelling areas west of South America and of Africa, whereas extremely clear water was encountered in the Sargasso Sea.

During the "Galathea" Expedition measurements of the light penetration into the sea were made at all stations where ordinary measurements of organic productivity were made. It was thus not possible to restrict the measurements to days when the light conditions and other weather conditions were absolutely favourable.

The ship was not very well fitted for measurements of submarine light. In a wind, the "Galathea" quickly gathered leeway on account of the very high superstructure. As a result, routine measurements could not be made further down than about 40-50 m, and for greater depths is was necessary to extrapolate. The measurements made during the "Albatross" Expedition made it possible to make such an extrapolation adequately. It must be stressed, however, that the measurements made on the "Galathea" by no means equal the measurements made on the "Albatross" in quality.

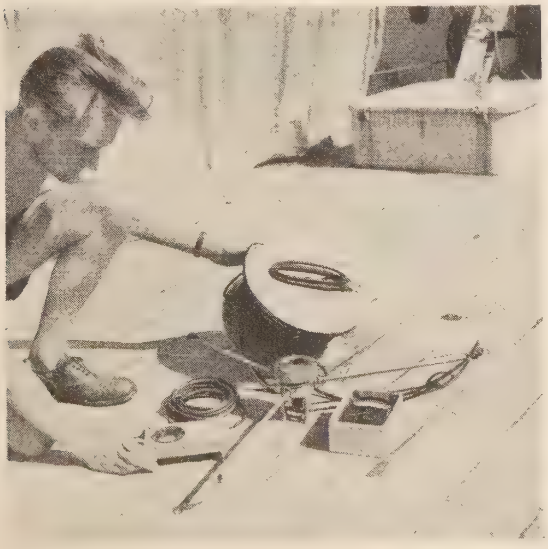

Fig. 15. Submarine photometer.

When the weather conditions were favourable the "Galathea"-measurements gave results which were practically identical with the "Albatross"-measurements in the same water. In the Sargasso Sea the Swedish Expedition made investigations at the two stations 372 and 377 – Jerlov 1951. Blue light (465 mμ) was found at a depth of 40 m. in percentages of 36 and 35 respectively of the intensity just below the surface. At three "Galathea"-stations in the Sargasso Sea the light conditions were favourable; 760, 762, 763. Blue light of practically the same wave length was observed at a depth of 40 m. in percentages of 38, 34 and 32 respectively of the intensity just below the surface.

Measurements had to be made also during much less favourable light conditions, however. The precision is therefore not always very high. However, the light measurements were only made with the purpose of determining the vertical extension of the photosynthetic layer. As no great precision was aimed at here – cf. p. 62 – the light measurements during the "Galathea"-Expedition may be considered adequate. The lower boundary of the photosynthetic layer was put at the depth at which the light is 1 per cent. of the total quantity of blue and green light at the surface – cf. p. 61. Only this depth is presented in table 20, as it may be considered misleading to publish all the details of the measurements.

For the measurement of light intensities the "Galathea" expedition used selenium photocells of a diameter of about 40 mm. which were manufactured by Evans Electroselenium Laboratory.

For submarine measurements the photocell was fitted in a watertight metallic casing provided with a thick glass window directly over the photocell – see Fig. 15. A rubber-insulated cable was introduced through a watertight stuffing box in the bottom of the casing and connected to the terminals of the cell. The casing was provided with three arms by means of which the photometer was connected through a crowfoot with three branches to the wire for lowering it into the sea. For measurements of light intensities above the surface of the sea, i.e. on deck, a photocell was fitted in a simple wooden mount which might be placed at any point where the illumination remained undisturbed by irrelevant factors.

The submarine photometer as well as the deck-photometer were arranged so that light filters might be fitted over the photocells. The filters used were manufactured by Chance Brothers and had the following denotations: red OR1, green OGr1, and blue OB10. In addition one or more neutral filters of the type ON31 were used.

It is recommendable to place a diffusing opal glass above all filters. This, however, is not very important for relative measurements not aiming at a high precision.

The weak photo-currents were measured by means of a sensitive moving-coil ammeter. The moving coil of this instrument is carried on pivots, and there are three measuring ranges with full scale deflections corresponding to 0.0001 amp., 0.001 amp., and 0.01 amp. respectively. For all three measuring ranges the internal resistance of the instrument is 300 ohms.

In the measurements made with the described equipment it was not possible to keep within the ranges in which the deflection varies directly with the illumination of the photocell. It was therefore necessary prior to the departure of the expedition to plot correction curves for the photocells to be used in connection with the measuring instrument. From these curves it should be possible for every deflection of the instrument to read a value which is proportional to the luminous flux incident on the photocell. It was not necessary to provide the instrument with a graduation in definite units, e.g. lux, as relative measurements only were aimed at.

The correction curves were plotted as follows: by means of an incandescent lamp, placed perpendicular to and in front of the photocell, the instrument was caused to give a deflection I_1 sufficiently small to be safely inside the range in which illumination and deflection are proportional. A neutral filter was now inserted in front of the photocell and the resulting, somewhat smaller, deflection I_2 was read. The ratio of one deflection to the other is then equal to the "filter factor" of this filter in the set-up concerned.

$$f = \frac{I_1}{I_2}$$

By increasing the illumination, while leaving the filter in front of the photocell, the instrument was again caused to give the deflection I_1. The filter was now removed, and the resulting deflection I_3 was read. The filter was again brought into position, the deflection caused to increase to I_3, whereupon removal of the filter resulted in a deflection I_4.

We now have four different deflections with the corresponding "relative illuminations", as follows:

deflection I_2 corresponds to illumination I_2
– I_1 – – – I_1
– I_3 – – – $f \times I_1$
– I_4 – – – $f^2 \times I_1$

By extending and repeating this procedure, a sufficiently large number of points were determined to enable the plotting of a curve representing the relationship between instrument deflections and relative illumination. In the case of deflections above 0.0002 amp. the curve shows a considerable deviation from linearity. The different photocells of the same type which were used for the measurements showed almost identical response, so that the same correction curve could be used for all of the photocells as long as they remained intact. During the work on board one photocell suffered slight damage necessitating special corrections subsequently to the few measurements made with this photocell.

The procedure applied during the measurements at the different stations was as follows: The measurements were made as near as possible to noon, and preferably in weather characterized by light air and thin clouds.

The vessel was stopped after having been manoeuvred into such a position that the stern with the rigged boom turned towards the sun.

The submarine photometer was fitted with colour filter and a suitable neutral filter ensuring that the instrument deflections were kept within the range covered by the correction curve. The deck-photometer was provided with the same filters and placed in full daylight. The submarine photometer was weighted with a 5 kg. lead weight and fastened by means of a shackle to the wire from a small hand winch at the boom. The photometer was now lowered into the sea, and measurements were made immediately below the surface and at four to six different depths down to 40 metres. On account of the considerable leeway it was only in few cases possible to make measurements at greater depths, because the wire angle became too large and the determinations of the depth consequently too inaccurate.

The rubber-covered cable from the photometer and the cable from the deck-photometer were both connected to the instrument on deck, the arrange-

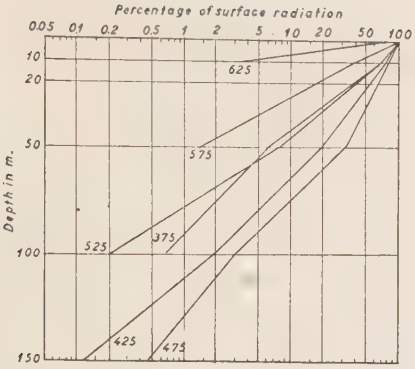

Fig. 16. Light penetration in the Sargasso Sea (After Jerlov).

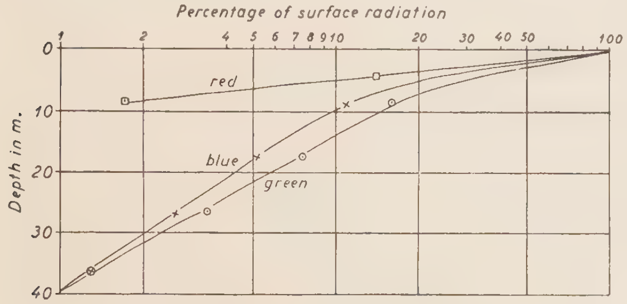

Fig. 17. Light penetration at St. 138. Benguela Current.

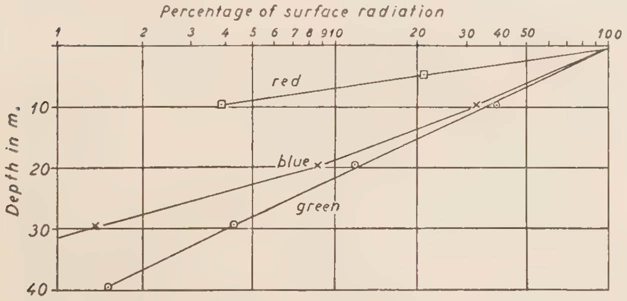

Fig. 18. Light penetration at St. 109. South Atlantic, off Angola.

ment being such as to enable a very rapid change-over of the instrument from one photometer to the other.

The following procedure was applied during the reading: at each depth the deflection produced by the deck photometer was first read and immediately afterwards the deflection produced by the submarine photometer. The readings were repeated with each of the three colour filters fitted, and this completed the actual photometric measurements.

Figures 16-18 show examples of the penetration of light into the sea in areas with different transparencies. The measurements are discussed in Part 2. With respect to the clearest water (in the Sargasso sea) Jerlov's measurements have been used, since the corresponding Galathea measurements have only been continued to a depth of 40 metres.

A consideration of the results obtained show that in very clear water blue light will penetrate farthest, while green light exhibits the greatest penetration in more turbid water. Red light proves in all cases, except one in water very rich in plankton (Walvis Bay, St. No. 139), to have a very low power of penetration compared to blue and green light.

In the calculation of the depth of the productive zone the red light has consequently been neglected at all stations of normal character. The limit of the productive zone has been defined as the depth at which the sum of the blue and the green light is equal to 1 per cent of the same sum measured at the surface of the sea.

To calculate this depth a method was used based on the direct measurements, the results of which were the following:

depth in metres	blue light, µamp		green light, µamp	
	in the sea	on deck	in the sea	on deck
a	i_{vba}	i_{dba}	i_{vga}	i_{dga}
b	i_{vbb}	i_{dbb}	i_{vgb}	i_{dgb}
c	i_{vbc}	i_{dbc}	i_{vgc}	i_{dgc}
etc.				

By means of the photocell correction curves the measured currents have been converted in to figures which denote the relative light intensities. The following table is obtained:

depth in metres	blue light		green light	
	in the sea	on deck	in the sea	on deck
a	i_{vba}	i_{dba}	i_{vga}	i_{dga}
b	i_{vbb}	i_{dbb}	i_{vgb}	i_{dgb}
c	i_{vbc}	i_{dbc}	i_{vgc}	i_{dgc}
etc.				

Now all of the measurements made in the sea are referred to the same intensity of light incident on the surface (measured on the deck).

This results in the following expressions for the relative intensities in the sea at the different depths:

depth in metres	blue light	green light
a	$I_{vba} = B_a$	$I_{vga} = G_a$
b	$I_{vbb} \times \frac{I_{dba}}{I_{dbb}} = B_b$	$I_{vgb} \times \frac{I_{dga}}{I_{dgb}} = G_b$
c	$I_{vbc} \times \frac{I_{dba}}{I_{dbc}} = B_c$	$I_{vgc} \times \frac{I_{dga}}{I_{dgc}} = G_c$
etc.		

The aim is now to determine the depth x which satisfies the following equation:

$$B_x + G_x = \frac{B_o + G_o}{100} \qquad \text{I}$$

The calculation is based on Beer's law:

$$\log \frac{I_a}{I_b} = k\,(b - a)$$

where I_a and I_b are the light intensities at the depths a and b, and k is the extinction coefficient. By substituting the intensities of blue light at the different depths, we find the extinction coefficients $k_{B(a,\,b)}$, $k_{B(b,\,c)}$, etc. In most cases these values do not differ much, and an extinction coefficient is consequently calculated by integration from the result of the uppermost measurement and that of the deepest measurement. The extinction coefficient thus found is denoted k_B. The extinction coefficient k_G for green light is calculated correspondingly.

The intensity of the green light and that of the blue light at the surface of the sea may be taken to be approximately identical. In order to find the total power of penetration of blue and green light we use a common extinction coefficient for light of these two colours which we calculate as follows:

$$k_{B+G} = \frac{k_B + k_G}{2} \qquad \text{II}$$

The result obtained by this method is not theoretically correct, and particularly when k_B and k_G differ much the result will be somewhat erroneous. For the purpose of the present measurements in which we do not aim at any very great accuracy the error is, however, negligible. The depth at which 1 per cent of the blue-green light is left can now be calculated from the following equation:

$$\log \frac{B_x + G_x}{B_o + G_o} = k_{B+G} \times x \qquad \text{III}$$

Combining this with equations I and II, we obtain

$$x = \frac{4}{k_B + k_G} \qquad \text{IV}$$

When blue and green light has been measured at the same depths a and b, we have:

$$k_B = \frac{\log \frac{B_a}{B_b}}{b - a} \quad \text{and} \quad k_G = \frac{\log \frac{G_a}{G_b}}{b - a}$$

and by substitution in equation IV we obtain

$$x = \frac{4\;(b - a)}{\log \dfrac{B_a \times G_a}{B_b \times G_b}} \qquad \text{V}$$

From this formula it is possible to calculate x directly from the corrected measurements. The depths a and b were determined by measuring the length of wire paid out by means of a meter wheel. At wind forces above 3 (Beaufort's scale) the leeway made by the vessel was sufficient to cause the wire angle to be considerable. In such cases the wire angle (the angle the wire rope makes with the vertical) was measured and the depth measurements corrected accordingly.

As already mentioned 40 metres was the maximum depth at which measurements of light intensities were made. However, at many of the stations the measurements of the extinction coefficients showed that the depth at which 1 per cent remains of the blue-green light considerably exceeds 40 metres. In these cases it has been necessary to extrapolate from the measurements made up to 40 m., the extinction coefficient being assumed to remain constant also at depths beyond 40 metres.

It has been shown, however, that this assumption is not correct. Jerlov (1951) has shown the absorption curves (in semilogarithmic representation) of clear sea water to display a break at about 40-50 metres, the extinction coefficient of the lower layers being higher than that of the upper layers.

This deviation is fairly high, and allowance was consequently made for it in the evaluation of measurements made in very clear water.

On the basis of Jerlov's measurements the following corrections have been calculated for all values of x from 60 metres and to 150 metres.

x (calculated) m.	correction %	x corrected m.
150	– 20	120
140	– 18	115
130	– 16	109
120	– 14	103
110	– 12	97
100	– 10	90
90	– 8	83
80	– 6	75
70	– 4	67
60	– 2	59

The calculation of the plankton production has been based on values of x calculated and corrected as described in the above.

H. LIMITATIONS AND PRECAUTIONS IN USING THE ^{14}C-TECHNIQUE

All methods have their limitations. Thus also the ^{14}C-method. Some important hints concerning the necessary precautions to be taken are repeated here:

(1) Because of the intermixing of photosynthesis and respiration it is only possible with reservations to make measurements if the rate of respiration equals the rate of photosynthesis. The latter rate must preferably at least be twice the rate of respiration, and the measurements are of a rather low quality even under this condition. A minimum ratio 4:1 is necessary in order to get a high accuracy. Therefore measurements by the ^{14}C-technique must be made at a high light intensity where natural phytoplankton normally shows a high ratio between the rate of photosynthesis and the rate of respiration, cf. p. 56. "In situ" measurements must be made during the day only and they must not be extended right down to the compensation depth.

(2) The measurements must be of short duration but not too short, due to a possible after-effect of light inhibition. "In situ" experiments must last only half a day, in the Tropics thus about 6 hours. At longer experimental times the quality of the measurements decreases.

With few exceptions all the water samples used in the experiments were collected in the period from about 2 hours before noon to about 2 hours after noon. At the start of the experiments with surface water we therefore must expect a more or less pronounced depression in the rate of photosynthesis. This is also seen in the experiments showing the dependence of the photosynthetic rate on the length of the experimental time. According to Fig. 6a, p. 57, the rate of photosynthesis was distinctly lower during the first hour as compared with the rate during the succeeding four hours. The experiment was started one hour after noon. It is suggested that the initial depression in the photosynthetic rate of surface samples is only of minor importance – although of some – if the duration of the experiments is four hours. The results of the experiments with surface water thus also seem to agree rather well with those in which water was used from the depth where only 10 per cent. of the surface light was found and where consequently no light inhibition was found. The slightly higher potential rate of photosynthesis often found at this depth as compared with that at the surface is primarily caused by the fact that the standing crop of phytoplankton is highest a little below the surface; cf. p. 110. Due to vertical mixing the effect of light inhibition at the very surface mostly is somewhat reduced.

(3) In laboratory experiments exceeding more than some few hours the experimental water must be stirred permanently as otherwise i.a. photo-oxidation may give trouble.

(4) When making tank experiments the temperature in the tank must be close to the temperature in the sea. Some plankton algae are sensitive to sudden changes in temperature.

(5) In waters with a relatively high content of bacteria and other heterotrophic organisms it is imperative to make control experiments in black bottles. A high ratio of the counts from the filters may under such conditions be due to dark fixation by the bacteria.

(6) The filters must be treated with fuming hydrochloric acid in order to get rid of possible inorganic carbon, e.g. in coccoliths.

(7) When measuring the organic production by placing the experimental bottles at the surface of the sea or in a tub on deck, it must be considered that the results may be very dependent on the weather conditions. In bright weather the rate of photosynthesis is lowest; cf. p 102.

I. COMPARISON BETWEEN RESULTS OBTAINED BY THE ^{14}C-TECHNIQUE AND BY OTHER TECHNIQUES. THE RATIO BETWEEN GROSS PRODUCTION AND NET PRODUCTION

STEEMANN NIELSEN 1952 compared results obtained by the carbon-14 technique with results obtained by using the ordinary light-and-dark bottle O_2-technique (Winkler titrations). The correction to be introduced in the carbon-14 technique was computed at the same time. A culture of *Scenedesmus quadricauda* was used. According to the basic composition of *Scenedesmus* cells and to the fact that in the culture solution nitrogen was added as nitrate, the oxygen method was regarded as giving a 33 per cent. greater yield than the carbon-14 method.

A multitude of experiments in which either algal cultures or natural plankton populations from Danish lakes were used have corroborated the original experiments. The same was the case in similar experiments made by RYTHER 1954, who writes, p. 134: "In general, agreement between the two techniques was extremely good. While photosynthesis values obtained by the ^{14}C method were consistently lower, they were always within 50-90 % of those obtained by light-and-dark bottle oxygen experiments." As RYTHER used a CO_2/O_2 exchange quotient of 1 and did not introduce any correction for ^{14}C-discrimination and for the intermixing of photosynthesis and respiration his experiences are in full agreement with those obtained in this laboratory.

MYERS and JOHNSTON 1949 found a CO_2/O_2 exchange quotient between 0.70 and 0.76 in photosynthesis of rapidly growing *Chlorella pyrenoidosa* with nitrate as the nitrogen source. They suggested that a value of 0.9 commonly reported from short-time manometric measurements is due to a temporarily increased carbohydrate synthesis when *Chlorella* is suddenly exposed to high light intensity.

As the basic composition of plankton algae from nature generally hardly deviates very much from that of *Scenedesmus* and *Chlorella* it seems reasonable to use a CO_2/O_2 exchange factor of 0.75 when expressing measurements obtained by the oxygen technique in equivalents of carbon.

As an example showing the extremely good agreement between the carbon-14 technique and the oxygen technique, measurements from a Danish Lake – Furesø – are presented. The rate of production is sufficiently high in this lake to produce measurements of a high quality by using the oxygen technique. NYGAARD 1955 has presented measurements from the lake made during a whole year, 1950-1951. The gross production was 675 g. glucose per m^2 per annum. The maximum rate was 5.21 g. per m^2 per day. The ordinary oxygen technique was employed. The experimental bottles were suspended throughout the whole photosynthetic layer. During the year 1953-1954 similar measurements were made with the carbon-14 technique during all months in three localities in the Furesø. One of the localities corresponds to the locality where Nygaard had made his observations. The gross production there was 209 g. C per m^2 per annum. The maximum rate was 1.40 g. C per m^2 per day.

If Nygaard's measurements are converted to carbon and a CO_2/O_2 exchange quotient of 0.75 is used, we obtain a gross production of 204 g. C/m^2 per annum and a maximum rate of 1.56 g. C/m^2 per day. The two years were rather similar regarding weather conditions. It is, however, striking to find such an extremely good agreement.

Numerous measurements with the tracer technique in the Danish Waters and in the Arctic have in the same way shown a good agreement with previous measurements with other techniques. These will be published elsewhere.

In the present paper all production values have been given as gross production values. The main reason for converting the direct measurements obtained by the tracer technique – being intermediate between the gross and net production – into gross production instead of net production is the fact that the oxygen technique is only able to produce reliable gross production values because of the presence of animals and heterotrophic plants. It is of importance to be able to compare the results obtained by using the two different techniques.

Relying primarily on experiments with net plankton STEEMANN NIELSEN 1937 suggested that the maximum rate of photosynthesis in phytoplankton collected directly from the sea mostly is about 20 times the rate of respiration. The daily rate of respiration by the phytoplankton in the photosynthetic layer below a surface unit was on this basis put at 15 per cent. of the daily rate of photosynthesis below the same surface unit. In computing the net production for all oceans, RABINOWITCH 1945 also corrected for 15 per cent. respiration losses.

Steemann Nielsen 1951 in presenting rather intensive studies on the production of organic matter in a Danish fjord discussed the matter again. It was concluded that the net production per surface unit on the average was 75 per cent. of the gross production. The same conversion was used for the oceanic production by Steemann Nielsen 1952.

The present authors still believe that a rate of net production being 75 per cent. of the rate of gross production must be considered rather adequate for the oceans in general. None of the numerous experiments on the dependence of the photosynthetic rate on light intensity both made during the "Galathea" Expedition – cf. p. 101. – and in Danish and Arctic waters have been inconsistent with such a supposition. For formal reasons a slightly higher correction for the respiration losses has nevertheless been used in the present paper. If the rate of photosynthesis at optimum light intensity is 10 times the rate of respiration, the latter rate must be about 20 per cent. of the rate of photosynthesis per 24 hours at the depth where the rate of photosynthesis is highest. For the whole photosynthetic layer the rate of respiration therefore is about 40 per cent. of the rate of photosynthesis – cf. p. 89. The rate of net production per m^2 surface is thus 60 per cent. of the rate of gross production. With the exception of the winter season at high latitudes the correction for respiration losses just presented must be considered maximum.

PART II. THE MEASUREMENTS OF ORGANIC PRODUCTIVITY

A. GENERAL INFORMATION

The route of the "Galathea" around the world was from west to east. Investigations were made in all oceans. As one of the main objects of the expedition was to investigate the bottom fauna of the deep trenches found in the oceans, the route was planned so that as many of these trenches as possible could be visited. During the first part of the expedition a special task was stressed, namely to make quantitative investigations of the bottom fauna along the whole of the Atlantic coast of Africa. The range of action of the ship was somewhat limited. The size of the fuel tanks allowed only certain special ocean crossings.

The distribution of the oceanic stations at which measurements of organic productivity were made is thus far from being ideal. Important material was nevertheless gathered during the expedition. It must be kept in mind that the measurements were pioneer work.

B. THE ATLANTIC OCEAN

(The chart, fig. 19)

The Atlantic is the ocean by far best known concerning phytoplankton. In the subtropical and tropical parts of the ocean particularly the "Deutschland" Expedition and the "Meteor" Expedition have collected important material concerning the standing crop of the phytoplankton – cf. p. 50. The hydrographic conditions – including nutrient salts – in the Atlantic must be considered relatively well investigated also.

Although the "Galathea" investigations of organic productivity cover only rather limited parts of the ocean, it seems possible to give a rough, general picture of the production of organic matter in the ocean. The high correlation found between the standing crop of plankton, according to the counts made by Hentschel on the "Meteor", and the measurements of organic productivity made during the cruise of the "Galathea", makes it possible to use measurements of the standing crop for estimation of the rate of production – cf. p. 79.

An outline of the hydrographic conditions in the Atlantic is found in Sverdrup et al. 1942. Only some scattered remarks will be given in the present work. The North Atlantic and the South Atlantic are both characterized by large circulating current systems; in the South Atlantic these run counterclockwise and in the North Atlantic clockwise. In the South Atlantic the Benguela Current is running in a northerly direction along the west coast of South Africa. It receives a material part of the water masses from subsurface layers. The upwelling of water from middle depth is of particular importance close to the shore. The mean temperature at the surface in February – the hottest month of the year – just outside the former harbour of Swakopmund (latitude 23° S) is only 17.1°C. Going further out into the current the temperature rises. It is, however, still relatively low thus showing the influence of the upwelling water.

The South Equatorial Current crosses the South Atlantic in a westerly direction just south of the Equator. A part of the current runs into the North Atlantic combining here with water masses from the North Equatorial Current. Another part – the Brazil Current – continues in a southerly direction along the coast of South America. The central part of the South Atlantic at middle latitudes constitutes a big anticyclonic counterclockwise eddy.

A similar anticyclonic eddy, the Sargasso Sea, is found in the North Atlantic. On the Northern Hemisphere, the direction is clockwise. The North Equatorial Current starts near Africa, where pronounced upwelling occurs off the coast. The current flows across the ocean and a part of it enters the Caribbean Sea; another part is the Antilles Current running just east of the West Indies. Between the North Equatorial Current and the South Equatorial Current a countercurrent running in an easterly direction is found. North of the central eddy the eastgoing Atlantic Current is found, a continuation of the Florida Current.

The "Galathea" Expedition started its work in the Atlantic. During October-December 1950 the ship worked along the whole of the African coast from south of Gibraltar to Cape Town. At more than 50 stations the rate of organic production was measured. The main work of the expedition during this period was to make comparative bottom inve-

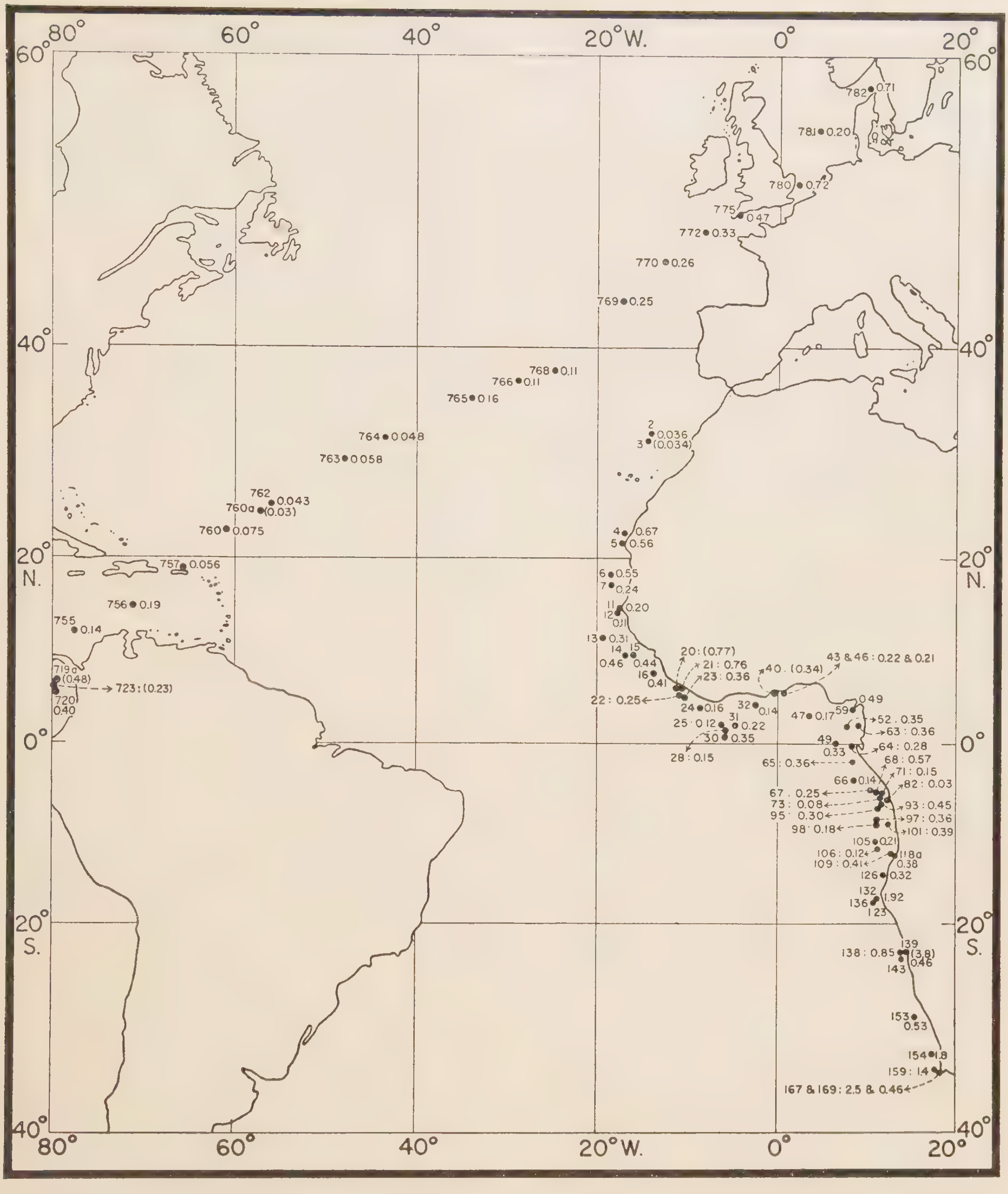
80°
60°
40°
20°W.
0°
20°
60°
40°
20° N.
0°
20° S.
40°
782●0.71
781●0.20
780●0.72
775●0.47
772●0.33
770●0.26
769●0.25
768●0.11
766●0.11
765●0.16
764●0.048
763●0.058
2 ●0.036
3●(0.034)
762 ●0.043
760a●(0.03)
760●0.075
757●0.056
756●0.19
755 ●0.14
719a ●(0.48)
723: (0.23)
720 0.40
4●0.67
5●0.56
6●0.55
7●0.24
11 ●0.20
12 0.11
13●0.31
14 15
0.46 0.44
16● 0.41
20: (0.77)
21: 0.76
23: 0.36
22: 0.25
24●0.16
25: 0.12
31 ●0.22
30●0.35
28: 0.15
32●0.14
40: (0.34)
43 & 46: 0.22 & 0.21
47●0.17
59●0.49
52: 0.35
63: 0.36
49 0.33
64: 0.28
65: 0.36
68: 0.57
71: 0.15
66●0.14
82: 0.03
67: 0.25
73: 0.08
95: 0.30
93: 0.45
97: 0.36
98: 0.18
101: 0.39
105●0.21
106: 0.12
109: 0.41
118a 0.38
126●0.32
132 1.92
136 1.23
139 (3.8)
138: 0.85
143 0.46
153● 0.53
154●1.8
159: 1.4
167 & 169: 2.5 & 0.46

Fig. 19. Measurements in the Atlantic Ocean. Station numbers on the left, organic production (g. C per m.² per day) on the right. The values are in brackets at stations where only measurements of surface water were made.

stigations near the coast. The route was therefore not specially suited for measuring oceanic productivity in the eastern part of the Atlantic. As the "Meteor" plankton counts present an excellent supplement to the productivity studies it seems nevertheless possible to give a not too bad picture of the organic production.

1. The Area off North Africa

Stations 2 and 3 north of Teneriffa represent the outskirts of the oligotrophic water found to the west but at least in autumn, reaching as far east as Teneriffa. The water was very transparent. The depth of the photosynthetic layer was more than 100 m.

The rate of production was accordingly low, about 0.04 g. C/m.^{2}/day.

Stations 4 – 24 were situated in the eutropic area near the westcoast of North Africa. Some are found on the shelf, others over great depth until 200 miles off the shore. As may be seen clearly also from the investigations of the "Meteor" (HENTSCHEL 1933, Beilage I) the conditions for plankton production are somewhat complicated in the area in question. According to Hentschel the centre of the area with maximum concentration of plankton was found about 20°N, 20°W. The same centre was evidently found during the "Galathea" Expedition. It is rather likely however, that seasonal fluctations play at least some role. In general it may be stated that the area is very productive. This has also been stated concerning zooplankton, e.g. during the "Dana" Expedition (cf. JESPERSEN 1935, Fig. 27 and 28).

2. The Gulf of Guinea

In this gulf, Hentschel showed (cf. Fig. 20, p. 78) a characteristic quantitative distribution of the plankton. The Guinea Current (the most eastern part of the Equatorial Countercurrent) was easily recognizable as a relatively plankton-poor water mass. Less than 10.000 cells per litre in 0-50 m depth was counted here by Hentschel. To the South, the broad, so-called Congo tongue carrying relatively plankton-rich water (more than 10.000 cells per litre in 0-50 m depth) is found. It reaches far out into the middle of the ocean. The breadth of the tongue is about 5 latitudes. South of the tongue, relatively plankton-poor water approaches the coast of Africa. The tongue is comparable with the plankton-rich water just south of the Countercurrent in the eastern part of the Pacific – cf. pag. 88 – and is at least partly due to the divergence found.

The Guinea Current (Stations 24, 25, 28, 31, 32 and 47) is also recognizable as an area relatively poor in organic production. Per m.^{2}, the production varied from 0.12 to 0.22 g. C/day. At Station 30 just south of this area – i.e. in the Congo tongue – the production was 0.34 g. C/m.^{2}/day. This station, however, has a common feature with the stations in the Guinea Current. The surface water is poor in organic production. At Station 30, the photosynthetic rate of surface water at 18.000 lux was 0.28 mg.C/m.^{3}/hour. At the stations in the Guinea Current it varied between 0.14 and 0.26. In a water sample from a depth of 40 m., the rate at Station 30 (18.000 lux) was 1.1 mg.; at the stations in the Guinea Current in water from this depht, the corresponding rate varied between 0.39 and 0.70/m.^{3}/hour.

In the lower part of the photosynthetic layer which extended downwards to about 70-80 m., and in the water-masses immediately below, high concentrations of phosphate were found everywhere. At a depth of 80 m. the concentration of phosphate varied between 1.0 and 1.8 μg.-atom P/L.

By the turbulence produced for example by the currents due to the internal waves – cf. p. 00 – nutrients are thus easily contributed to the photosynthetic layer. The water near the surface seems not to benefit much from this supply of nutrients however. Our knowledge about the mixing rates of the water-masses in the surface layers is unfortunately very limited. It is easy to understand however, that in areas of this kind where the mixing, for some reason or other, increases, the conditions for organic production improve too. The Congo-tongue represents according to all evidence such an area.

The stations over shallow depths in the Gulf of Guinea were characterized by a fairly moderate production rate. The highest value was found in the innermost corner at Port Victoria (0.49 g. C/m.^{2}/day).

The coastal area outside the Gold Coast is characterized during a part of the year by upwelling water – see e.g. the chart, Beilage III, HENTSCHEL 1933 after Meyer, according to which such an upwelling is found in February. This must have a decisive influence on the production rate here at that time of the year.

3. The area outside the Congo-Estuary

The influence of the huge water-masses carried out by the Congo is distinctly to be seen far off shore both by the decrease in salinity and by the lowering of the transparency of the water – see table 4. Station 66, 210 miles off the coast and 260 miles north west of the mouth of the Congo, was thus characterized by a surface salinity of 32.59‰ and a depth of the photosynthetic layer of only 22 m. The low transparency was not due to a big standing crop of plankton. The production rate per m.^{2}/day was only 0.14 g. C and the rate at 18.000 lux per m.^{3} of the surface water was only 1.23 mg. C/hour. The relatively low salinity at Stations 97 and 98 is presumably also caused by the Congo; it is hardly due to water coming from the Quanza River which de-

Table 4. Stations outside the Congo-Estuary.

Station no.	Distance in miles from mouth of the river	Salinity ‰	Depth of photosynthetic layer in m.	Production at 18.000 lux of surface water mg.C/m.^{3}/hour	Production in the whole photosynthetic layer g.C/m.^{2}/day
65	320	34.04	45	0.86	0.36
66	260	32.59	22	1.23	0.14
67	180	29.43	10	4.8	0.25
68	70	28.73	6	15.9	0.57
71	40	25.99	5	5.1	0.15
73	30	23.93	4	3.8	0.08
82	10	18.78	5	0.89	0.03
93	60	34.27	50	1.28	0.45
95	100	34.36	39	0.93	0.30
97	150	33.30	35	0.90	0.36
98	170	34.77	32	0.86	0.18

bouches just south of Loanda. Station 101 situated about 60 miles nearer the coast had a salinity of 35.05. If the relatively low salinity at Stations 97 and 98 should have been caused by water from the Quanza River, the influence at Station 101 should have been still more pronounced.

No investigations were made in the estuary proper. It must be supposed that the vertical turbulence here in connection with the opaqueness of the river water makes any production of organic matter by plankton algae practically impossible.

In the mixing area outside the river mouth the conditions are different. Although the water masses at least near the surface are very opaque the high degree of stabilization must prevent vertical turbulence rather effectively. Organic production is thus going on near the surface. At Station 82, where the lowest salinity – 18.78‰ S – was found, only a relatively low rate of photosynthesis was found in surface water illuminated by 18.000 lux. As the depth of the photosynthetic layer was only 5 m. the production per surface unity was extremely low – 0.03 mg. C/m.^{2}/day. It is likely that one of the main reasons for the low potential photosynthesis of the surface water at Station 82 is the very recent formation of this water by the mixing of river water and surface sea water. Both kinds of water are poor in plankton algae. The freshwater species, if any, may further be considered unable to stand a salinity of 18‰. It takes some time for establishing a considerable plankton population. It was impossible to determine inorganic phosphates in the surface water due to the intense yellow colour. At a depth of 10 m. where the salinity was 35.50‰ S and thus showing no indication of any mixture with the river water, the phosphate concentration was 0.3 μg-atom P per litre. At stations 67,68, 71 and 73 the salinity at the surface varied between 29.43 and 23.93 ‰ S. The potential photosynthesis of surface water was relatively high. The rate at 18.000 lux varied between 3.8 and 15.9 mg.C/m.^{3}/hour, the highest rate being found at a salinity of 28.73‰, the lowest rate on the other hand at Stations 73 at a salinity of 23.94‰. This is a further indication of the fact that it takes some time after the start of the mixing before a considerable stock of plankton algae is found. No inorganic phosphate was found at the surface at Station 73.

Due to the low transparency at all of the stations mentioned above the rate of production as measured per m.^{2} surface is not particularly high with the exception of Station 68, where 0.57 mg. C/m.^{2}/day was measured in spite of the photosynthetic layer being only 6 m. deep.

4. The area north of the Benguela Current proper

The rate of organic production in the area just north of the Benguela Current (North of latitude 15°S) was found to be much lower than in the Current proper. The area constitutes a natural continuation of the Benguela Current. However, no upwelling of subsurface water to the surface takes place here, at least at the time of the year – November – when "Galathea" visited the area. Stations 101-126 belong to this area. Stations 97 and 98 situated about 40 miles more to the west than St. 101 may be included too. Due to the influence of Congo-water which is distinct according to the surface salinity at both stations, they were treated jointly with the stations from the area outside the Congo-Estuary. With respect to the rate of organic production Stations 97 and 98 were in according with the other stations in the area just north of the Benguela Current. The rate varied between 0.12 and 0.41 g. C/m.^{2}/day. The two stations with a relatively low production – Stations 105 and 106 – were situated about 50 miles from the coast over a depth of about 4000 m. The other stations were situated near the coast over a depth less than 1600 m.; Station 118 lay in the entrance to the Bay of Lobito where the depth was only 30 m.

The depth of the photosynthetic layer was fairly small at all stations – 34 – 43 m (21 m in the Bay of Lobito). The low transparency particularly at Stations 105 and 106 may seem a little astonishing considering the relatively low rate of production. No big standing crop of phytoplankton seems to have been present lowering the transparency to that extent. It must, however, be taken into account that the surface water of the area in question has its origin in more southern latitudes where a very high plankton production is going on constantly. Despite the relatively low standing crop of phytoplankton the water presumably contains much detritus and "Yellow substance" remnants from a previous very high production.

Hentschel 1933 p. 90, has called attention to another similar phenomenon from the regions near the African coast. The areas here showing the highest concentration of the herbivoreous zooplankton organisms do not, according to the "Meteor" investigations, coincide absolutely with the areas where most phytoplankton was found but are displaced in the direction of the current; "so dass man versucht ist zu denken, dass eine stärkere Entwicklung des Metazoenplanktons auch räumlich auf die Hauptentwickling des Nannoplanktons folgt."

It seems perhaps reasonable therefore to assume that the rate of organic production in the area is controlled to a higher degree than normally by grazing. According to the hydrographic conditions a somewhat higher rate of photosynthesis could perhaps have been excepted. At a depth of 40 m., which is just in the lowermost part of the photosynthetic layer in the region, at least 1.7 μg-atoms P/l. (inorganic) was found at all stations. At a depth of 30 m. the concentration of inorganic phosphate varied between 0.1 and 0.4 μg-atoms P/l.

Seasonal fluctuations are presumably of importance in the present area. The hydrographic conditions indicate that even small variations may have a serious influence on the phytoplankton.

5. The Benguela Current

The Benguela Current is known to be one of the most productive areas of the oceans – cf. e.g. Hentschel 1933. The current flows along the west coast of South Africa and is particularly conspicuous between the southern extremity of Africa and latitude 17° to 18°S (Sverdrup et al., 1942, Clowes 1950). Under the influence of the prevailing southerly and south-easterly winds, the surface water is carried away from the coast, and upwelling of water from moderate depths takes place in most seasons of the year. These hydrographic conditions give rise to an enormously rich phytoplankton, since the upwelling water is rich in nutrient salts and establishes excellent conditions for plankton production.

Table 5.

	Depth in m	S ‰	°C	μg-atom P/l	Production at 18.000 lux mg.C/m.^{3}/hour
St. 138 depth of photosynthetic layer 39 m.	0	35.05	15.73	1.7	7.5
	15	35.10	12.48	2.3	0.92
	30	35.08	12.20	2.3	0.16
St. 143 depth of photosynthetic layer 37 m.	0	35.03	15.43	1.7	3.5
	15	35.01	13.73	1.7	1.1
	30	35.05	21.63	2.1	0.47

According to the "Galathea"'s measurements at 9 stations (132-167), the rate of organic production varied between 0.46 and 2.5 g. C/m.^{2}/day (in Walvis Bay 3.8 g. C). The lowest rate measured – 0.46 g. C – was found at Station 143 in the area where the highest rate of upwelling was demonstrated. Station 138 – organic production 0.85 g. C/m.^{2}/day – was situated in the same area. In table 5 the data about hydrography and production are presented.

At both stations a high, although not extremely high, potential photosynthesis was found at the surface. A similar high potential photosynthesis was not demonstrated below the surface. At a depth of 15 m. where the light conditions must have been excellent – cp. Fig. 17, p. 65 – such a high rate could have been expected. The low temperatures at depths of 15 and 30 m. at both stations indicate very recent upwelling of water masses from medium depths. The surface temperatures of 15-16 °C., on the other hand, is an indication that some heating has occurred, and some time must have elapsed since the water just at the surface rose. Water masses in the photosynthetic zone can be too "new"; it takes some time before a considerable population of plankton algae develops in the water masses brought up to the euphotic zone from the aphotic zone below (cf. Sverdrup and Allen 1939).

Fig. 17, p. 65 showing the percentage of surface radiation at the different depths at Station 138 indicates clearly that the subsurface water is much more transparent than the plankton-rich upper layer.

At Station 143 the same light conditions in the sea were found.

The position of Stations 138 and 143 is in the innermost part of the especially plankton-rich area called "die Südwestafrikanische Zunge" by HENTSCHEL 1933. This area stretches about 1000 miles out into the ocean. The richness in plankton is due to the upwelling immediately on the coast. It is therefore interesting to note that in the very place of upwelling the organic production is not particularly high. It was a pity that the time did not allow the "Galathea" to make a section out in the ocean at this latitude.

Fig. 18 from Station 109 gives a strikingly different picture. This is in accordance with the fact that the water from the subsurface is at least as plankton-rich as that from the surface; cf. Table 20, p. 125.

Another area with plankton-rich water stretching far out into the ocean was found by Hentschel near the southern limit of Africa – and called "die Kap-Zunge "by him. At two "Galathea"-stations near the coast in this area organic production was measured (Stations 154 and 167).

Per surface area, both stations had a high rate of organic production – 1.8-2.5 g. C/m.^{2}/day. In the centre of the upwelling area outside Cape Town a third station is found – Station 159. Due to insufficient recording of the measurements at the station it is only possible to state the rate of production with some reservation.

The observations made at only 9 stations in the entire area of the Benguela Current do not allow any detailed description of the organic production. Measurements during all seasons of the year are necessary in order to present a detailed picture.

6. Walvis Bay.

Walvis Bay (latitude 23 °S.) is known as a place where an enormous fish mortality often occurs (cf. e.g. COPENHAGEN 1953). This question will be thoroughly discussed by R. Spärck in another "Galathea" Report. The fish mortality is often – although not always – described as being due to red water i.e. a mass occurence particularly of naked peridinians. When the "Galathea" dropped anchor in Walvis Bay in order to celebrate Christmas Eve December the 24th, 1950, a fish mortality had occurred some days before. Red water – or better "khaki" water as a local man said – was found in the bay.

Only the water masses near the surface could, however, be called "khaki" or red. At midnight the water at a depth of 3,5 and 6 m. was quite clear, at 2 m. nearly clear, at 1 m. rather stained and at the surface very coloured. The colour was due to huge amounts of a little naked dinoflagellate which was handed over to Professor Braarud, Oslo, who has examined the alga and described it as a new species: *Gymnodinium Galathea* Braarud (see Braarud 1957).

Table 6. Hydrographic observations at the anchorage Walvis Bay. 24.12.50 (started 23 h 30').
Depth 6 metres.

Depth in metres	°C	S ‰	"O_2" ml./l.	Inorganic Phosphate µg-atom P/l.
0	19.80	35.26	0.86	> 2
1	18.03	35.14	1.44	> 2
2	17.93	35.10	2.34	> 2
3	17.03	35.07	2.94	2.3
5	16.66	35.05	2.33	2.1

Some other phytoplankton species – peridinians – were present without being of quantitative importance at all, however.

Light measurements at noon showed that 1 per cent. of the total green and blue light at the surface was found at a depth of about 0.8 m. Experiments with surface water yielded a gross production of 3.8 g. C. assimilated per square metre of the surface per day. This enormously great production took place in a water layer of 0.8 m. only.

In Table 6 the hydrographic data from the anchorage in Walvis Bay are shown. The observations were made just before and after midnight.

The temperature at the surface was distinctly higher in the bay than just outside. At Station 138 just outside the bay thus a temperature of only 15.73°C. was found at the surface. The salinity at the surface was also higher in the bay – 35.26 S‰ here against 35.05‰ at Station 138 – indicating a rather high evaporation in the bay.

Oxygen was determined in the usual way by means of the Winkler-method The 0.86 ml./l. at the surface apparently shows a distinct undersaturation. This can hardly be correct, however, as the intense photosynthesis in the surface layer produces enormously great quantities of oxygen, establishing in all probability a definite supersaturation of oxygen.

According to the measurements of photosynthesis, more than 10 ml. O_2/litre was produced by the surface water during the day whereas less than 1 ml. O_2 must be supposed to have been used during the respiration going on from sunset to midnight when the O_2-determinations were made. The great quantity of phytoplankton does not seem to allow the use of the Winkler-method. The present determination gives a striking example of the inexpediency of using the Winkler-method as a standard method in very eutrophic water.

In the present case it is presumed that a part of the iodine produced corresponding to the amount of free oxygen is absorbed by fatty oils in the algae. Fatty oils having double bonds will loose these in the presence of iodine. For each double bond two atoms of iodine will be absorbed.

Considerable concentrations of inorganic phosphate were found at all depths. In the surface-layer 0-2 m. the amounts are given as minimum values, as an exact determination was impossible because of the enormous amounts of plankton present. At least 2 μg-atom P/l. were present at the surface. If the ratio P: C is put at 0.02 (Cooper 1937), and the assimilation of the 3.8 g. C per square metre is assumed to have taken place in the uppermost metre (0.8 m. according to the measurements of the submarine light), presumably more than 2 μg-atom P/l. must have been taken up during the last day. At least 4 μg-atom P/l. must thus have been present on the morning of December the 24th, if no P has been added to the surface layer during the day. As the great plankton production had been going on for at least some days already, constantly using phosphate, a considerable quantity of this salt must be available in the bay.

Rivers from land will only sporadically convey considerable water masses to the bay. At the moment of the investigation this had not happened for a very long time. The sewage from the settlement in Walvis Bay is insignificant and cannot provide any phosphate enrichment of real importance in the bay.

From the bottom sediments amounts of phosphate are undoubtedly conveyed to the free water masses just as in similar localities. Due to bacteria, phosphate is regenerated from organic compounds in the bottom sediment. Such a contribution of phosphate cannot, however, without specifications, be the real source for the surface layer, since in this case a significant increase in phosphate from the surface where the algae are found exclusively, to the bottom should have occured. If anything, the opposite is observed. It is, however, possible that large quantities of phosphate are produced only at very shallow depths, thus affecting only the very surface water.

The water from the depth in the eastern part of the South Atlantic has a phosphate content of about 3 μg-atom P/l. at the most (see Thomsen 1937). During the cruise of the "Galathea", a phosphate content above 1.7 μg-atom P/l. at the surface was not observed. The red water in Walvis Bay can decidedly not have been due only to deep water being brought to the surface in the Benguela Current outside the bay. Such water would only have had phosphate enough for one or two days at the most when the uptake of P is about 2 μg-atom P/l. per day. As more than 2 μg-atom P/l. was "left" at the moment of investigation another explanation for the red water in the bay must be looked for.

A possible explanation besides that offered above seems to be phosphate supply through the guano given off by birds. During our visit, enormous swarms of sea birds were seen over the bay. It must be assumed that they had been fishing outside the bay at the rich fishing grounds there and were on their way back to their nests. December falls during the nesting time of the sea birds of this region. It is therefore explained at the same time why the red water in Walvis Bay always seems to occur at this time of the year.

The tide being about one metre in Walvis Bay will daily wash a considerable amount of guano from the beach at the places where the birds have their nests, thus presumably giving rise to a considerable concentrations of nitrate and phosphate in the surface water of the bay.

In calm weather as during the visit of the "Galathea" to Walvis Bay the population of the *Gymnodinium* is found only just at the surface down to about 1 m. If this alga produces a poison responsible for the fish mortality, this poison should thus be found only near the surface. During rough weather the wind will effect mixing of all water layers in the shallow bay however and thus give rise to a poisoning of all water masses in the bay. It may possible be assumed that such a mixing of the water masses is necessary in order to effect a real mass mortality of fishes. It is difficult by using the hydrographical material obtained during the stay of the "Galathea" in Walvis Bay to determine when the last vertical mixing of the water masses, if any, had occurred.

7. The Section across the North Atlantic Ocean.

Fig. 19 shows also the rates of organic production on the section from Panama to the English Channel. The section was run during May and June 1952. The first two stations – 755 and 756 – are situated in the southern part of the Caribbean Sea; Stations 757 and 760 in the Antilles Current, which is a westward continuation of the North Equatorial Current. Stations 762-764 are in the Sargasso Sea; Stations 765-772 in the North Atlantic Current, the last of the stations mentioned being situated on the continental slope. Station 775 lies at the mouth of the English Channel.

As may be seen e.g. from the excellent survey given by SVERDRUP *et al.* 1942, the surface water in the Caribbean Sea has its main origin in the North Equatorial Current, which at its western end carries fairly "old" surface water.[1] The main eddies in the Caribbean Sea affecting vertical mixing of the water masses are situated more to the north. In the southern part of this region oceanic productivity may therefore be expected to be of normal size. The rate was 0.14-0.19 g. C. per square metre per day.

The production of organic matter in the Antilles Current is poor, being only 0.056-0.075 g. C, which is in accord with the rather old "age" of the surface water.

About the lowest oceanic productivity anywhere found by the "Galathea" – 0.043-0.058 g. C per square metre per day – occurred in the Sargasso Sea. In this big anticyclonic eddy in mid-Atlantic the surface water is "old", and the same water circulates here for a fairly long time. The surface water of the eddy receives contributions from the sides, partly from the western end of the North Equatorial Current (carrying "old" surface water) and partly from the uppermost layers of the Gulf Stream. Owing to the anticyclonic nature of the eddy, which is situated in the northern hemisphere, there is a tendency for the surface water to descend near the centre (see fig. 7 – BÖHNECKE et al., 1930). This effect is to be seen in the distribution of the nutrient salts below the photosynthetic zone. Concentrations above 0.4 μg-atoms P per litre are first found several hundred metres below this zone, which in the Sargasso Sea reaches down to about 120 m. (see Table 12, p. 94 and "Dana" Stations 3540-3544 – THOMSEN, 1937). Thus only quite minimal amounts of the nutrient salts are conveyed to this zone by mixing with water from below the photosynthetic zone.

It is therefore readily understandable that the rate of organic production in the Sargasso Sea is low. This sea has long been regarded as a poor region, and the blue water there has been described as an oceanic desert. KALLE 1939 has shown that the content of suspended particles, according to the Tyndall effect in water samples, is exceedingly low in the surface water of the Sargasso Sea indicating a very low content of plankton algae such as shown by LOHMANN 1920 and HENTSCHEL 1933 by the use of a centrifuge. The paucity of the plant production is reflected also in the rate of animal production. The smallest volume of oceanic zooplankton reported by the Danish "Dana" Expedition round the world was found in the Sargasso Sea (see JESPERSEN, 1935). (The findings of Riley, who believes the Sargasso Sea to be a productive area, are discussed by STEEMANN NIELSEN 1954, 1955).

Stations 765-768, in the North Atlantic Current, represent a region of typically subtropical oceanic surface water of medium "age". The rate of organic production varied between 0.11 and 0.16 g. C per square metre per day. In the northwestern part of the Sargasso Sea near the border of the Gulf Stream similar conditions are possibly found during a part of the year due to seasonal fluctuations in the admixture of Gulf Stream water to the area. As one approaches the European continent, organic productivity increases – probably due to the activity of the eddies found here. At Station 772 the production rate was 0.33 g. C per day.

Finally, a productivity of 0.47 g. C per square metre par day was found at Station 775, in the mouth of the English Channel. If production occurs here at this rate throughout the months of March to June, the result will be a productivity of the same order of magnitude as was estimated by the Plymouth Laboratory from the decrease of phosphate from spring to summer (ATKINS, 1923).

The "Galathea" continued to make observations in the English Channel and in the North Sea – cf. table 20. These observations will be discussed in another publication in connection with observations from later Danish cruises.

8. A survey of the Atlantic Ocean

The Atlantic Ocean is the most thoroughly investigated ocean in all respects. Because of the "Meteor"-Expedition the South Atlantic is particularly well known concerning the quantitative distribution of plankton. As the "Galathea" measurements on organic production are too few to permit the construction of a survey chart dealing with a whole ocean, the "Meteor" counts have been used as a supplement for designing such a chart. The very

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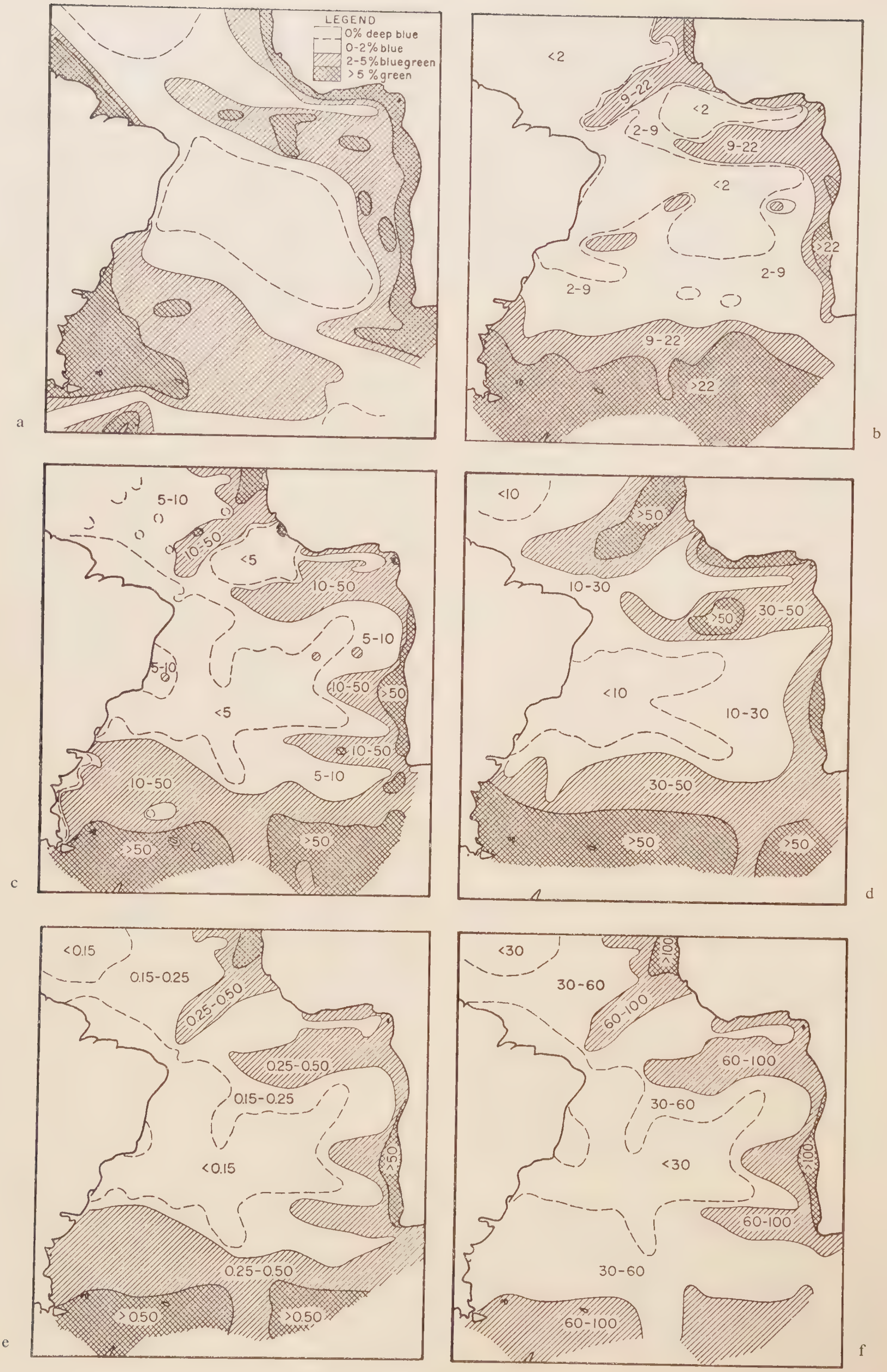
[1] The "age" of surface water is explained on p. 89.


LEGEND
0% deep blue
0-2% blue
2-5% bluegreen
>5 % green
a
<2
9-22
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2-9
9-22
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b
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10-30
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30-50
<10
10-30
30-50
>50
>50
d
<0.15
0.15-0.25
0.25-0.50
0.25-0.50
0.15-0.25
<0.15
>50
0.25-0.50
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>0.50
e
<30
30-60
>100
60-100
60-100
30-60
<30
>100
60-100
30-60
60-100
f

←— Fig. 20. A series of charts of the South Atlantic Ocean. a, distribution of colour of the sea (after SCHOTT); b, distribution of phosphate in mg per $m.^3$ in the upper 50 m. layer; c, distribution of plankton organisms, thousands per litre, in the upper 50 m. layer (after HENTSCHEL and WATTENBERG 1930); d, distribution of zooplankton (metazoa), numbers per 4 litre in the upper 50 m. layer (after HENTSCHEL 1933); e, distribution of organic gross production in summer (g. C per $m.^2$ per day; f, distribution of annual net production (g. C per m^2).

high correlation found between the standing crop of plankton algae and the production of organic matter – as will be shown in Part 3, – makes such a combination of data of different origin not only possible but quite obvious.

In Fig. 20 e a chart of the South Atlantic is presented showing the rates of organic gross production per day and per m^2 of the surface in the different areas. Whereas the rates presented for the tropical and subtropical parts of the ocean must be considered more or less representative for the whole year, this is not so for the areas outside the Tropics and Subtropics. The rate given for the areas south of Latitude about 35°S correspond only to the conditions during the middle of summer, when the maximum production is going on in these waters. For the whole year, the average rate of production is presumably only about $^1/_3$ of the rates found during the height of summer. Certainly the rate of annual organic production in the Atlantic Ocean is considerable, but not nearly as high as would appear by taking only the summer conditions into account.

In Fig. 20 f a chart of the South Atlantic is presented showing the annual net production per m^2 of the surface in the different areas. Although many assumptions are necessary in order to estimate the annual rates outside the Tropics and Subtropics, the chart most likely may be considered satisfactory as a first approximation. In principle all other oceans are supposed to resemble the South Atlantic Ocean.

According to Fig. 20, b and c, we find an extraordinarily high correlation between the standing crop of plankton and the concentration of phosphate near the surface. The latter may on the other hand easily be correlated with the general hydrographic conditions. High concentrations of phosphate near the surface are only found in areas where a considerable addition of subsurface water to the surface takes place. The central part of the ocean – the big anticyclonic eddy – is on the other hand characterized by a downward movement of the surface water. Very little inorganic phosphate is therefore here at the disposal of the plankton algae, the concentration of which consequently is low.

The charts presented in Fig. 20 are discussed in detail in Part III.

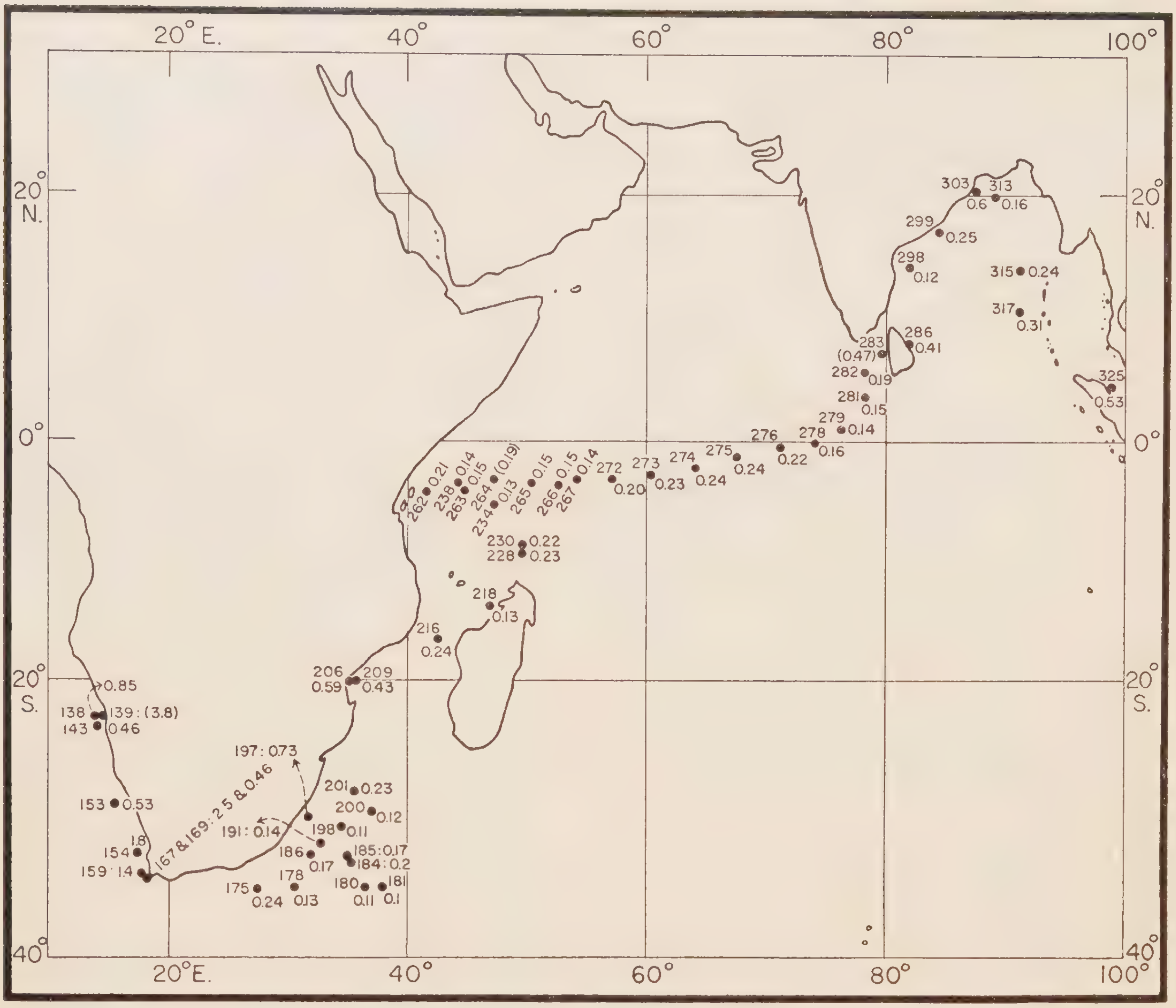
C. THE INDIAN OCEAN

(The charts, Fig. 21 and Fig. 26)

Previous investigations of importance for evaluating the productivity of the Indian Ocean have been made particularly by the "Dana" Expedition 1928-1930, the "John Murray" Expedition 1933-34, the "Swedish Deep-Sea Expedtion" 1947-48 and the "Discovery" Expedition 1934. GILSON 1937 has used the nitrate determinations from the "John Murray" Expedition for estimating the production of organic matter in the Indian Ocean. He arrived at a production rate of 14.4 g./$m.^2$/day (wet weight of algae). It is, however, hardly realistic to use the method employed by this author for estimating organic productivity. The value will not be considered in the present treatise.

The main lines of the hydrography of the Indian Ocean may be found in SVERDRUP *et al.* 1942. In general terms they may be sketched as follows. During all seasons there is found a typical South Equatorial current starting at Australia and flowing across the Ocean south of the Equator. On reaching Africa, a part of it turns south and follows the African coast. The most southerly continuation is called the Agulhas Current. In the southernmost part of the Ocean a current starts south of Africa and is going in an easterly direction towards Australia. In the center of the currents metioned is found an anticyclonic eddy, similar to the eddy found, e. g., in the South Atlantic.

North of the Equator is found in parts of the year the westgoing North Equatorial Current; this, however, is neutralized when the South West Monsoon is blowing, or is substituted by an eastgoing current. Between the North Equatorial Current and the South Equatorial Current a Counter Current is found. The southern boundary of this current is found between 9°S and 5°S. Off the African coast the northern boundary is situated at about 4°S. "The Swedish Deep-Sea Expedition" made special investigations regarding the Equatorial Currents and the Counter Current in the Indian Ocean (JERLOV 1953).


20° E.
40°
60°
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100°
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0°
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303
313
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299
0.25
298
0.12
315 0.24
317
0.31
283
(0.47)
286
0.41
282
0.19
281
0.15
279
0.14
278
0.16
276
0.22
275
0.24
274
0.24
273
0.23
272
0.20
325
0.53
262 0.21
238 0.14
263 0.15
264 (0.19)
234 0.13
265 0.15
266 0.15
267 0.14
230 0.22
228 0.23
218
0.13
216
0.24
206
0.59
209
0.43
0.85
138
139: (3.8)
143
0.46
153 0.53
197: 0.73
167 & 169: 2.5 & 0.46
191: 0.14
201 0.23
200 0.12
198 0.11
1.8
154
159 1.4
186
0.17
185: 0.17
184: 0.2
178
0.13
175
0.24
180
0.11
181
0.1

Fig. 21. Measurements in the Indian Ocean. Station numbers on the left, organic production (g. C per m.^{2} per day) on the right. The values are in brackets at the stations where only measurements of surface water were made.

1. The western part of the ocean

According to the investigations of the "Discovery" in the western part of the ocean, the distribution of phosphate in a very instructive longitudinal section in the Indian Ocean is given – Fig. 22 after Clowes 1938. The values are corrected for salt error according to Cooper 1937. In lower latitudes only a shallow surface layer poor in inorganic phosphate is found. In middle latitudes – 20°-35°S – this surface layer poor in nutrients is vertically extended. Whereas in the lower latitudes water rich in nutrients is found in the lower part of the photosynthetic zone giving rise to an important photosynthetic capacity here, in middle latitudes nutrient rich water is first found well below the lower boundery of the photosynthetic zone. The "Dana" investigations covering both nitrate and phosphate, and the phosphate observations made during the "Galathea" Expedition, confirm the "Discovery" investigations fully (cf. Thomsen 1937 and fig. 24 and fig. 25). In identical subsurface water the P observations by the "Dana" and the "Discovery" are fairly identical. The P values given by the "Discovery" in the most P-rich intermediate water are about 10 per cent. lower than

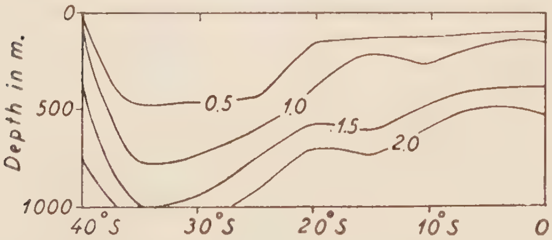


Fig. 22. The distribution of phosphate (μg-atom P/l) in a longitudinal section in the western part of the Indian Ocean (after Clowes 1938).

those presented by the "Dana". No investigations on the distributions of nutrient salts and plankton have been made in the central part of the Indian Ocean at middle latitudes. The big anticyclonic eddy situated here must be supposed to resemble the similar eddy in the South Atlantic in respect to the vertical distribution of the nutrient salts. Due to the descending of surface water in these anticyclonic eddies nutrient rich water is first met far below the lower boundery of the photosynthetic zone – cf. p. 77.

It is thus to be expected that a section out from Africa at middle latitudes should show the smallest rate of production to the east. The "Galathea" section along latitude 35°S – Stations 175, 178, 180, 181, illustrates this clearly. The production rate at Stations 181 – the most easterly station – was 0.097 g. C/m.^{2}/day. It was the lowest value found in the Indian Ocean by the "Galathea", although it is nearly the double of the values found in the centre of the corresponding eddy in the North Atlantic. Station 181 is, however, only situated near the boundary of the eddy.

All the "Galathea" stations at middle latitudes in western part of the Indian Ocean outside the continental shelf were characterized by a production rate between 0.1 and 0.2 g. C/m.^{2}/day, the value normally found in tropical and subtropical oceanic regions in abscence of any pronounced admixture of nutrient-rich water from below.

On the shelf itself, a pronounced ascent towards the surface of relatively nutrient-rich water from middle depth is found without, however, giving rise to any real upwelling of water to the very surface. The surface temperature was high everywhere. Station 197 off the coast of Natal gives a typical example. As on the "Galathea" only hydrographic observations were made in the photosynthetic zone, the Fig. 23 will be presented instead. It shows the distribution of P-PO$_4$ in a section off Africa at about latitude 28°S. The two stations located over the shelf are "Dana"-stations from January. The most eastern station is from the "Discovery" section (April) presented in Fig. 22. The ascent of subsurface water over the shelf is very significant. It is, however, not as considerable as in the Equatorial region of the Indian Ocean where, at least in the divergences, 1 μg-atom P is met with in a depth of 40-100 m. – cf. Fig. 22. Near the coast in the latitudinal section at 28°S, 1 μg-atom P/1. was found between 400 and 500 m.

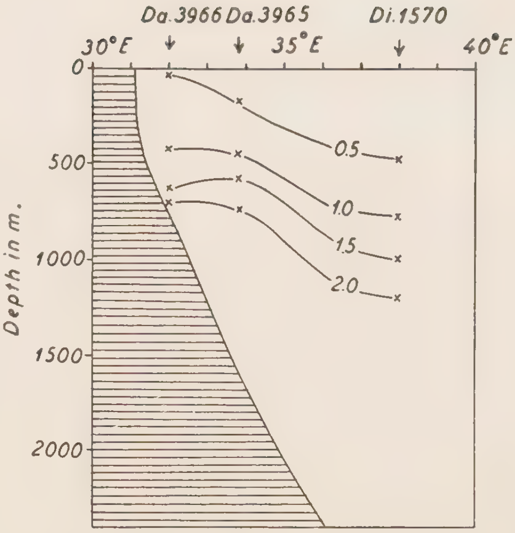


Fig. 23. The distribution of phosphate (μg-atom P/l) in a section off Africa at about latitude 28°S.

The lower boundary of the photosynthetic layer was at a depth of 30 m. at Station "Galathea" 197. Nutrient-rich water is thus conveyed into the photosynthetic layer – as also distinctly seen from the measurements at Station 197 – cf. Table 20. The high rate of photosynthesis in the surface water – 5.0 mg. C/m.^{3}/hour at 18.000 lux – shows that considerable amounts of the nutrients must be supplied rather constantly to all water masses in the photosynthetic layer. However, only small amounts of the nutrients are found at the very surface. 10 degrees more to the north at 20°S, similar conditions for the production of organic matter are found on the shelf-Stations 206 and 209. The rates were 0.59 and 0.43 g. C/m.^{2}/day respectively.

On the Agulhas Bank at the southern limit of the continent, a really considerable admixture of nutrient rich subsurface water to the surface was shown. Nitrate was found in concentrations up to 25 μg N-NO$_3$/1 at the surface – "Dana" Station 3972. The strength of the south-going Agulhas Current, the continuation of the South Equatorial Current, has apparently the effect that the ascent of deeper water masses already takes place above rather considerable depth. Thus at the "Dana" Station 3971 at 35°49'S, 23°09'E, where the depth was 1980 m 5 μg-atom N-NO$_3$/1 and 0.3 μg-atom P/1 was found at a depth of 75 m. At the "Galathea" Station 175 situated more to the east and over a depth of 4500 m., a distinct ascent of nutrient rich water into the photosynthetic layer was observed. The lower boundary of this layer was found at a depth of 81 m.; 1.7 μg-atom P/1 was measured at a depth of 75 m. Water from 80 m. had a photosynthetic rate of 0.88 C/m.^{3}/hour when illuminated by

18.000 lux. This is a rather high value, $3^1/_2$ times as high as the corresponding rate of the surface water, which was of the same size as found elsewhere east of Africa at these latitudes.

2. The Equatorial part of the ocean

Rather intensive investigations of organic productivity were made by the "Galathea" in the Equatorial part of the Indian Ocean. First of all a section from Mombasa to Ceylon was made. A preliminary survey of this section was already published during the expedition – Steemann Nielsen 1952. As already pointed out in the text of the article mentioned, the values given in the accompanying Fig. were about 30 per cent. too low owing to an exchange of the special Geiger-tubes used.

As shown by Jerlov 1953, the hydrographic conditions are complicated in the region in question. The vertical inhomogenity of the photosynthetic layer contributes further to complicate the measurements of organic productivity. Whereas the photosynthetic rate if, measured at 18.000 lux, mostly is rather uniform throughout the whole of the photosynthetic layer in the tropical and subtropical parts of the ocean, this is not quite true in the area in question. Photosynthetic rates up to 3 times the rate of surface samples at the same light intensity are often met with. Nutrient-rich water is found in the lower part of the photosynthetic layer, which in the area in question may have a vertical extension down to about 90 metres. The distribution of inorganic P and N-NO_3 at the 4 sections across het equatorial currents – Fig. 24 and Fig. 25 – shows this clearly.

The depth of the photosynthetic layer e.g. at Station 276 was 92 metres. The rates at 18.000 lux of water samples from 0, 40 and 80 metres were 0.24, 0.60 and 0.52 mg. C/m.^{3}/day respectively. The influence of the nutrients at the lower depths is obvious. In areas of the present kind it is preferable to take samples from more depths than three if a high accuracy is aimed at. It must further be expected that the extrapolations for the whole photosynthetic layer of the light measurements, which on the "Galathea" were made only down to 40 m. must be considered as being rather inexact in the area in question. The light measurements made during the "Swedish Deep-Sea" Expedition – cf. Jerlov 1951 – shows that in the area in question ("Albatross" Stations 201, 206, 227) the transmission of light is definitely decreased below a depth of about 30 m. (Fig. 23 of the paper mentioned). The vertical extension of the photosynthetic layer is therefore presumably estimated a little too high, hardly, however, more than 10 per cent. No attempts at making any corrections have been made. The accuracy when using the tank-method is less in this sort of water than normally. The order of magnitude of the determination, the really important matter during a pioneer work like the present, is of course not influenced.

The direction of the section of the "Galathea" across the Indian Ocean is not very suitable for in-

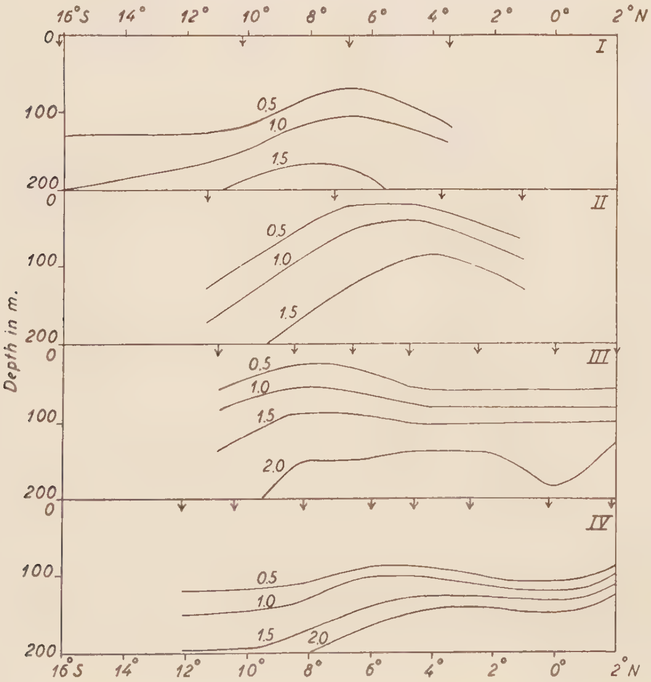
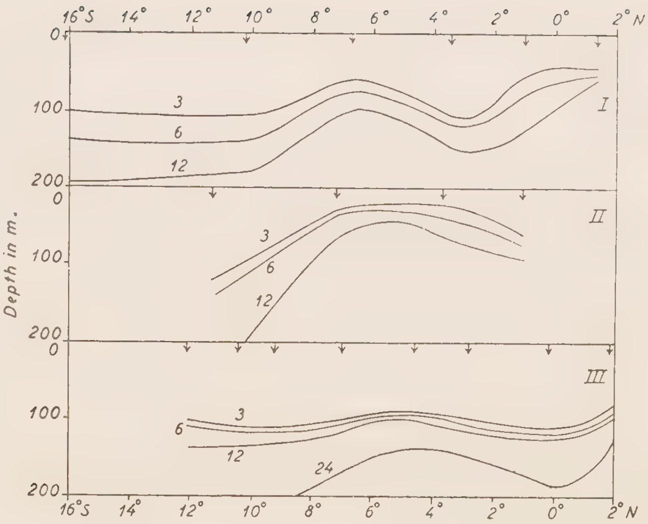


Fig. 24. The distribution of phosphate (μg-atom P/l) in four sections across the Equator (Indian Ocean). Section I at about longitude 40°-45°E. (Dana), Section II at longitude 50°-60°E. (Dana). Section III near 88°E. (Swedish Deep-Sea Expedition), Section IV near latitude 95°E. (Dana).

Fig. 25. The distribution of nitrate (μg-atom N/l) in three sections across the Equator (Indian Ocean). Section I at about latitude 40°-45°E., Section II at latitude 50°-60°E., Section IV near latitude 95°E.(Dana).



vestigating the details concerning the influence of the hydrographic conditions. The lack of data from depths below the photosynthetic layer must also be mentioned.

4 sections across the equatorial currents in the Indian Ocean are presented instead showing the vertical distribution of P-PO_4 and N-NO_3 in the upper water layers – see Fig. 24 and Fig. 25. Section I near Africa follows longitude about 40°-45°E. It is drawn according to the observations of the "Dana" – Dec.-Jan. 1929/1930. The nitrate data from the most northern part of the section not visited by the "Dana" are, however, taken from the "John Murray" Expedition, Dec. 1933 – Gilson 1937. The same method for determining nitrate was used on both expeditions. At some stations more to the east covered by both expeditions the results were conformant.

Section II is made according to the "Dana" observations between 50°E and 60°E. This section could not be extended to the north using data from the "John Murray" expedition. The nearest station was more than 8 latitudes more to the north than the most northern "Dana" station. 2 stations taken during the first mentioned expedition were situated in the middle part of the "Dana" section – about lat. 2°-3°S.

Section III near 88°E is from the "Swedish Deep-Sea" Expedition, Jerlov 1953 b. Only phosphate determinations were made. Section IV near 95°E originates from the "Dana".

The "Discovery" longitudinal section from the western part of the Indian Ocean presented in Fig. 22 crosses the Equator between Section I and Section II. In principle it is very similar to the other sections.

The shape of the isolines both for phosphate and nitrate shows for all sections at least one distinct divergence, where phosphate – and nitrate-rich water is found relatively near the surface. In Section 1 a divergence was found at about 7°S. 1 μg-atom P-PO_4 and 12 μg-atom N-NO_3 per liter were determined in the water from a depth of about 100 m. Another divergence was demonstrated at about 2°N according to the nitrate observations. No phosphate data are available from the northern part of the section. The southern divergence is found near the boundary of the South Equatorial Current and the Counter Current. The northern divergence must represent the northern boundary of the Counter Current. At about 3°S a convergence was demonstrated, 1 μg-atom P-PO_4 and 12 μg-atom N-NO_3 being found in a depth of about 150 m. Although the isolines for N and P are found at a somewhat greater depth in the convergence compared with the conditions in the divergences, they are nevertheless localized at a definitely higher level than, e. g., in the southern part of the South Equatorial Current. At 16°S the 1 μg-atom P/l. isoline was found at a depth of 200 m.

In section II only a southern divergence at about 5°S could be demonstrated. No observations were available in the area where a northern divergence could be expected. The descending of the isolines north of latitude 4°S indicates presumably the existence of a convergence just south of the Equator. 1 μg-atom P/l. and 12 μg-atom N/l was found at a depth of 40 m. in the centre of the divergence.

In Section 3 according to Jerlov 1953 one divergence is found near 8°S. Another should be found near the Equator and a convergence should be located at 4°S. According to the phosphate observations only the southern divergence is conspicuous. 1 μg-atom P-PO_4/l. was here found at a depth of 60 m.

In Section 4 a southern divergence is found at about 5°S. Another is found about 2°N with a very inconspicuous convergence lying between. In the divergences the isolines for 1 μg-atom $P\text{-}PO_4$/l. and 12 μg-atom $N\text{-}NO_3$/l. were found at a depth of 100 m.

From the 4 Sections showing the distribution of phosphate and nitrate it is obvious that nutrient-rich water is found rather near to the surface in the whole of the equatorial region of the Indian Ocean. This is true not only in the divergences but also in the convergences. In the central part of the ocean – see Sections 2 and 3 – this water is approaching nearest to the surface. The lower part of the photosynthetic layer must be supposed to provide good conditions for the plankton algae with respect to nutrients. The upper part of the photosynthetic layer may also profit by this nutrient-rich water just below. It must, however, be mentioned that a very high temperature gradient is found. In the centre of the divergence found in Section 2, the surface temperature was 8°C higher than that at a depth of 50 m.

The stations on the "Galathea" Section from Mombasa to Ceylon show a pronounced maximum of production between 57°E and 72°E. The reason for the smaller rate of production west of this region – Station 262 over the shelf is an exception of course – is apparently found in the decisively less ascent towards the surface of water rich in nutrient salts in the most western part of the ocean, as shown in section 1, Fig. 22 and Fig. 23. At Stations 228 and 230 in the South Equatorial Current just south of the divergence a relatively high production rate – 0.22-0.23 g. C/m.^{2}/day was found.

The four stations from the most easterly part of the Mombasa-Ceylon Section – 278-282 – are situated in the North Equatorial Current. Nutrient-rich water is still found rather near the surface. The 0.5 μg-atom P curve is found at a depth of about 50 m., a little higher up than in the Counter Current – cf. Sections 2 and 3, Fig. 24. The rates of production found were, however, a little lower than the rates in the Counter Current. Station 283 at the coast of Ceylon – depth 820 m. – had a production rate of 0.47 g. C/m.^{2}/day. As always in the Tropics, the production rate over the shelf increases.

According to SCHOTT, 1935, the Counter Current bends south at about 100°E and follows the coast of Java, its southern boundary not crossing 10°S until at 115°S. The "Galathea" Stations 466, 472, 475 were located here (fig. 26). At Stations 472 and 475 the rate of production was very high, 0.70 and 0.59 g. C/m.^{2}/day. Such high values were not found elsewhere in the tropical currents of the Indian Ocean. The photosynthethic layer was shallow, 34 and 40 m. respectively. Relatively cold water was found rather near the surface – cf. table 20, p. 125 –. The temperature was 23.4°C at a depth of 30 m. at Station 472. Thus an important conveyance of surface water into the productive zone explains the high rate of production. The topography of the bottom is presumably the most important factor causing the ascent of deeper water layers in this area. The depth at the two stations mentioned was about 2500 m. At Station 466, which was located 4 degrees further to the west, the depth was more than 7000 m. The rate of productivity was here only 0.17 g. C/m.^{2}/day. The lower boundary of the photosynthetic layer was, however, at a depth of 59 m, indicating that productive water was found not far away. The extension of this layer was reaching much deeper at the tropical stations in the western part of the Indian Ocean.

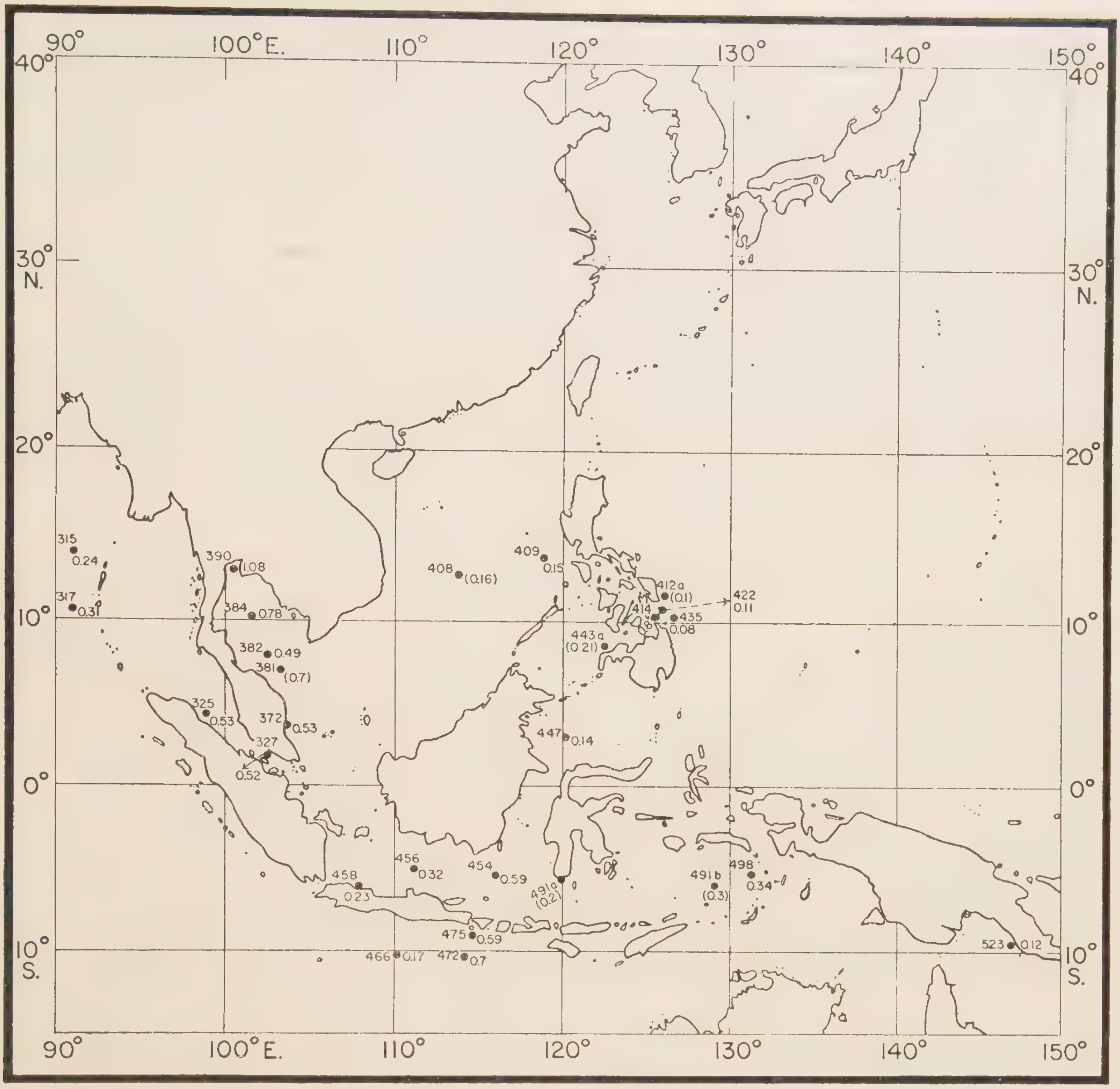
Summarizing all of the "Galathea" measurements in the equatorial current systems of the Indian Ocean, it seems reasonable to state that the rate of production is moderately high in the whole region. Only in locally very restricted areas was a very high production rate found.

3. The Bay of Bengal

The Bay of Bengal is a proper part of the Indian Ocean. Through supply of freshwater, the salinity is relatively low – about 33-34‰ at the surface. 4 stations were taken by the "Galathea" outside the shelf in this area. The production was on the avarerage 0.19 g. C/m.^{2}/day (0.12-0.24), a little more than usually found in tropical oceanic water.

Subsurface water rich in nutrients was found rather near to the surface at the two most northern stations. 3 μg atom P/l. was thus found at a depth of 80 m. at Station 299, and at a depth of 40 m. the concentration was 1.3 μg-atom P/l. The thickness of the photosynthetic layer was only 45-66 m. at the two western stations. At the two stations in the eastern part of the bay the lower boundary of the photosynthetic layer was at 84 and 99 m. respectively. Organic and inorganic material conveyed by the Ganges is presumably the reason for the relatively low transparency of the water in the western part of the Bay. The low transparency decreases the rate of photosynthesis as measured per surface area.

The three stations located on the shelf – 286, 303,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10° S.
315
0.24
317
0.31
390
1.08
384
0.78
382
0.49
381
(0.7)
325
0.53
372
0.53
327
0.52
408
(0.16)
409
0.15
412a
(0.1)
422
0.11
414
0.8
435
0.08
443a
(0.21)
447
0.14
456
0.32
454
0.59
458
0.23
491a
(0.2)
491b
(0.3)
498
0.34
475
0.59
466
0.17
472
0.7
523
0.12

Fig. 26. Measurements in the Indo-Malayan Waters. Station numbers on the left, organic production (g. C per m.^{2} per day) on the right. The values are in brackets at stations where only measurements of surface water were made.

315 – were all characterized by a high rate of production.

We may assume that the Monsoon shift has some influence on the rate of production in the Bay of Bengal. Extensive investigations during the different seasons are necessary in order to give a true picture of the production of organic matter.

4. The Indo-Malayan Waters

(The chart, Fig. 26)

Measurements of the rate of production in this huge area were made at altogether 13 complete stations and in addition at 4 surface stations. It is therefore possible only to give a very rough sketch of the conditions. The measurements were, however, rather instructive. Two of the three complete stations located over great depth – Station 409 in the northern part of the East China Sea and Station 447 in the Celebes Sea, resemble in all respects normal stations in the open oceans. The rate of production was 0.15 and 0.14 g. C/m.^{2}/day respectively. The depth of the photosynthetic layer was 98 and 90 m. respectively. Really nutrient-rich water was not found in the lower part of the photosynthetic zone. At a depth of 100 m. a concentration of 0.2 μg-atom P/l/day was found at Station 409. At Station 447 the concentration was 0.4. The results from "surface

Stations" 408 and 443 a resembles in all respects those from the complete stations from the same area.

Station 498 in the Banda Sea – depth 7465 m. – was very different from the four stations just mentioned. 1.3 µg-atom P/1. was found at a depth of 60 m. The depth of the photosynthetic layer was 42 m. The rate of production was 0.34 g. C/m.^{2}/day (the same rate was found at the surface station 491 b. The position of Station 498 was practically identical with "Dana" Station 3676 – cf. THOMSEN 1937. – Although this stations was taken in March and the "Galathea"-station in September the vertical distribution of nutrient salts is very alike. As the positions of the two stations are very near to the 1000 m. curve in the northwestern part of the Banda Sea, the conditions here are perhaps somewhat locally conditioned. The macroplankton-samples from the two "Dana"-stations from the Banda Sea, JESPERSEN 1935, indicate a not very high, but at least a somewhat higher production here than in the Celebes Sea and in the northern part of the East China Sea.

All of the 10 stations taken over shallow depth in the whole of the Indo-Malayan region were characterized by a high rate of production varying between 0.24 and 1.08 g. C/m.^{2}/day. On the average the rate was 0.61 g. C/m.^{2}/day. It was found during the expedition that the rate of organic production is high practically anywhere in the Tropics in shallow water.

D. THE PACIFIC OCEAN

(The charts, Fig. 26 and Fig. 27)

The investigations by the "Galathea" include scattered measurements in the most western part of the ocean, measurements in the Tasman Sea and the water around New Zealand, a section across the whole of the ocean from New Zealand to San Francisco and a section along the American Continent from San Francisco to Panama.

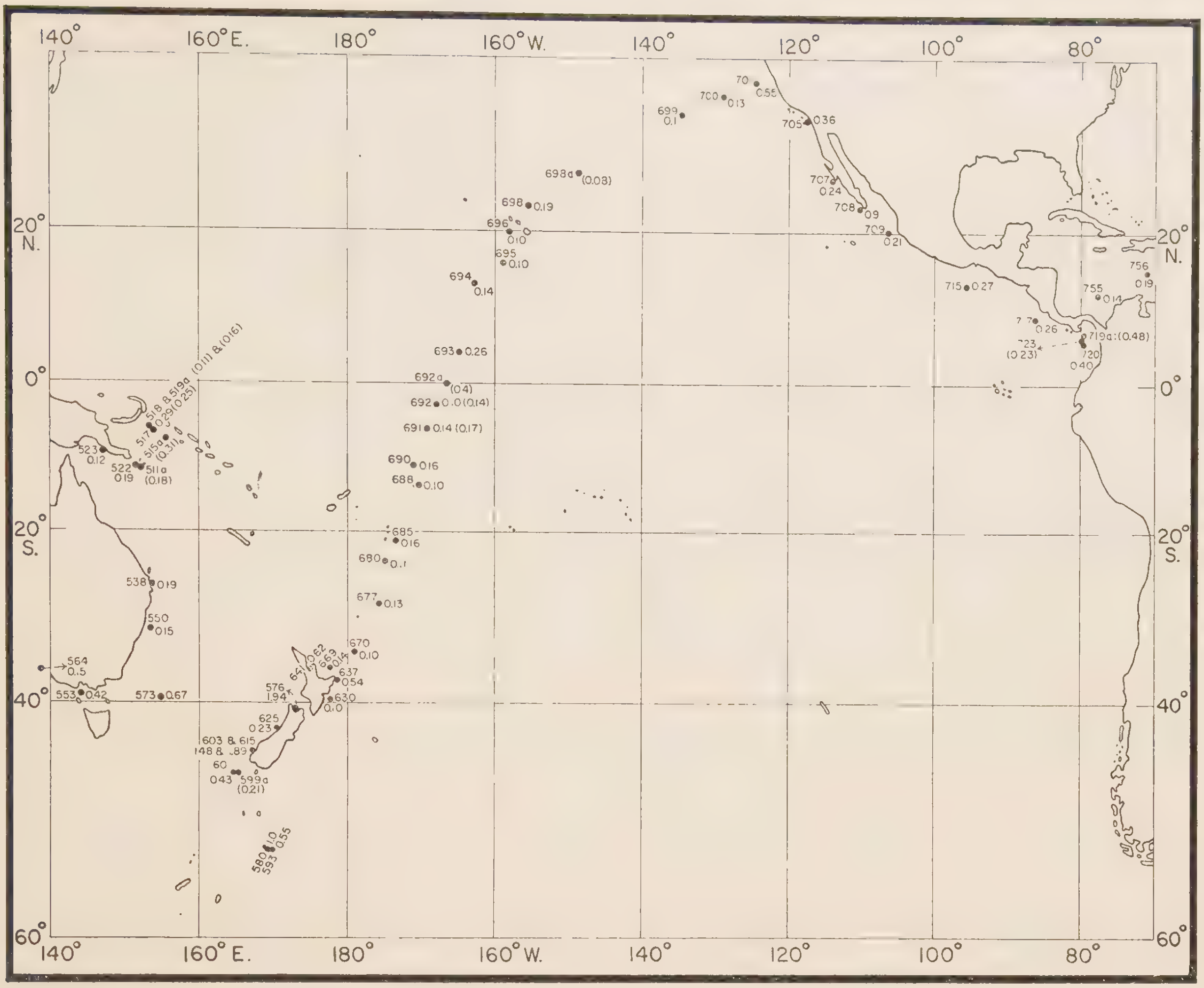
Despite the fact that the few "Galathea"-observations cover only a very small part of the big Pacific Ocean and despite the fact that the hydrography of just this ocean is but little known – cf. SVERDRUP *et. al.* 1942. – the measurements represent a not too bad introduction into the exploration of the organic production of this ocean. A few general rules may at least be laid down if the information from the other oceans is used as a supplement.

Stations 422 and 435 are located near the Philippines, Fig. 26, the first over the submarine slope-depth 2200 m., the other above the Philippine trench – depth 10.026 m. The rate of production was low at both stations, 0.11 and 0.08 g. C/m.^{2}/day respectively. The low rate of production is in accordance with the considerable vertical extension of the photosynthetic layer. The area in question may perhaps be compared with the area of the Antilles Current in the Atlantic Ocean, where a similar low rate of production was found – cf. p. 77.

West and south of New Guinea, measurements of the production were made on three normal stations and on four "stations" where only the rate of photosynthesis in surface samples was measured. The rate of production varied between 0.11 and 0.32 g. C/m.^{2}/day. Because of the Solomon Islands to the west and other islands, the hydrography of the area presumably must be rather complicated. It is not astonishing that both regions with a low productivity rate and regions with a decisively higher rate were found. The "Galathea" material is, however, quite inadequate for a closer study.

Three stations were taken in the coastal waters of Australia, Station 538 outside Queensland, Station 553 in the Bass Strait and 564 in the Great Australian Bight. Only in the Bass Strait was a really high rate of production measured (0.42 g. C/m.^{2}/day). It is, of course, impossible to say much about the productivity of the Australian coastal waters on the basis of this meagre material.

In the offshore waters of the Tasman Sea between Australia-Tasmania and New Zealand measurements were made at three stations. At Station 550 near the northern border of the Tasman Sea a rate of production of 0.15 g. C/m.^{2}/day was measured. This moderate rate is in accordance with the hydrographic conditions. No phosphate determinations were made at this station by the "Galathea". But according to the measurements of the "Dana" from January-February 1929, 0.5 µg-atom P/l. was first found at a depth of about 200 m. at the most western stations ("Dana" 3659 and 3663) of the section Auckland-Sidney. At the more eastern stations of the section, 0.5 µg-atom P/l. was found already at a depth of 75-100 m. – cf. THOMSEN 1937. According to the zooplankton measurements of the "Dana" – JESPERSEN 1935, Fig. 11 – a very distinct


140°
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698a (0.08)
698 0.19
696 0.10
695 0.10
694 0.14
693 0.26
692a (04)
692 0.0 (0.14)
691 0.14 (0.17)
690 0.16
688 0.10
685 0.16
680 0.1
677 0.13
670 0.10
637 0.54
630 0.0
662
669 0.14
641
576 1.94
625 0.23
603 & 615 1.48 & .89
60 0.43
599a (0.21)
580 1.0
593 0.55
518 & 519a (0.11) & (0.16)
517 0.29 (0.25)
515a (0.31)
523 0.12
522 0.19
511a (0.18)
538 0.19
550 0.15
564 0.5
553 0.42
573 0.67
70 0.55
700 0.13
699 0.1
705 0.36
707 0.24
708 0.9
709 0.21
715 0.27
756 0.19
755 0.14
7 7 0.26
719a (0.48)
723 (0.23)
720 0.40

Fig. 27. Measurements in the Pacific Ocean. Station numbers on the left, organic production (g. C per m.² per day) on the right. The values are in brackets at the stations where only measurements of surface water were made (St. 691 and St. 692 cf. Table 20, p. 134).

decrease in plankton volume in hauls with 50-100 metres wire, – 1½ m. stramin net – is found going from east to west in this section.

Stations 573 and 601 were located more to the south in the Tasman Sea, the former at 39°25′S, surface temperature 17.5°C, the latter at 45°51′S, surface temperature 12.7°C. Throughout the photosynthetic layer phosphate was present only in a concentration of 0.1 μg-atom P/l. at Station 573. Below the photosynthetic zone no phosphate determinations were made. The rate of organic production was high – 0.67 g. C/m²/day. There is reason to believe that the rate of production is seasonally conditioned. The station was worked on December 17th. In the middle of June-corresponding to the middle of December on the southern hemisphere – in the open Atlantic south of Iceland a dense phytoplankton is found. The spring maximum here starts during May – cf. Steemann Nielsen, 1935 and 1943 – after the commencement of stabilization due to the summer heating. There is reason to believe in at least some resemblance to the conditions in the temperate part of the Tasman Sea.

Station 601 was worked a month later in the south eastern part of the Tasman Sea. 0.4 μg-atom P/l. was found throughout the photosynthetic layer. The north-going current originating here from the adjacent Antarctic Ocean, where high phosphate concentrations are found at the surface during the summer (cf. Clowes 1938), indicates that a high rate of production presumably is going on here throughout the whole summer.

The "Galathea" measured the organic production in the waters near Campbell Islands south of New Zealand. One station was worked in the fjord Perseverance Harbour and one outside the fjord at a depth of 110 m. The rate of production was high on both stations – 1.0 and 0.55 g. C/m.^{2}/day respectively. This is in accordance with the concentration of phosphate found, 1.3 μg-atom P/l. at all depths in the photosynthetic layer.

In the shallow water around the coasts of New Zealand 7 productivity stations were worked by the "Galathea" in the period 21. December – 27. January. The rate of production was high everywhere, in the Cook Strait and in the fjord Milford Sound even extremely high. The coastal waters as well as the open waters around New Zealand are without doubt very productive. The zooplankton investigations by the "Dana" – cf. JESPERSEN 1955 Fig. 5 – also indicate this clearly. It must, however, be emphasized that investigations during all seasons must be made in an area like the present in order to obtain a correct picture of the productivity.

The section across the Pacific has already been discussed by STEEMANN NIELSEN 1954. Fig. 27 gives the rate of organic production in the section from New Zealand to California. The direction of the route was northwestward to Honolulu. From there the "Galathea" continued straight on to San Francisco. All stations were made between the beginning of March and the beginning of April, with the exception of Station 641, made at the end of January. This neritic station, at the mouth of Houraki Gulf, New Zealand and the last station of the section, Station 701, in the coastal water outside San Francisco, give a suitable contrast to the other stations of the section, which are all truly oceanic. The two neritic stations represent coastal areas with a high organic productivity – about 0.6 g. C per square metre per day.

The "Carnegie"'s last cruise in 1929, together with the "Dana"'s cruise, in 1928-1930 and the Swedish Deep-Sea Expedition 1947-1948 gives valuable information on the hydrography of the area in question (see SVERDRUP et al., 1942). The work done by the Fish and Wildlife Service at Hawaii in recent years has added much to our knowledge – cf. KING 1954, CROMWELL 1954, AUSTIN 1954. Between the North and South Equatorial Currents, in the east, there lies the remarkably well developed Equatorial Counter Current. The "Carnegie" found two regions of divergence in which the ascent of water from medium depths to the surface could be clearly recognized. One of these regions is situated in the South Equatorial Current near the Equator and the other on the northern boundary of the Counter Current. In these regions concentrations of slightly more than 0.4 μg-atoms P per litre were found at the surface. Net catches of plankton (GRAHAM, 1941) were also rich here.

The "Albatross" section – Stations 80-94 situated more to the East showed the same two divergences – JERLOV 1953, a, b. The "Galathea"'s section is further westward than the "Carnegie"'s. According to SVERDRUP *et. al.* (1942, Fig. 197) the depth of the discontinuity surface near the equator increases from east to west. This indicates perhaps a less pronounced admixture of water from medium depths on the "Galathea" section than on the "Carnegie" section. On the latter, between 8°S and 3°N concentrations of 0.4 μg-atom P per litre at the surface were found. On the "Galathea" section a phosphorus concentration of 0.3-0.7 μg-atom P per litre was, however, found at the surface at all stations between 6°S and 4°N. According to the 172° longitudinal section presented by CROMWELL 1954 0.5-0.8 μg-atom P per litre was found between 5°S and 5°N – February, March.

The rate of organic production was fairly uniform at the "Galathea"'s unfortunately relatively few stations on this section. With the exception of the stations near the divergence between the Counter-Current and the South Equatorial Current found just north of the Equator, the rate varied only between 0.10 and 0.19 g. C per square metre per day.

Only two stations were made by the "Galathea" in the region directly influenced by the divergence in question. The rates of production were 0.26 and about 0.4 g. C per square metre per day respectively. The last value is unfortunately not very exact. Only the productivity of the surface water was measured, since unfortunate circumstances made it impossible to carry out intensive investigations in this interesting locality. No influence on organic production of a possible divergence at the northern border of the Counter-Current was observed. This is in accordance with KING 1954 – cf. p. 118. JERLOV 1953a, Fig. 8 states a divergence near 10°N at his western section (Stations 124-138). The influence on the phosphate distribution was, however, very limited.

The thickness of the photosynthetic layer at the oceanic stations of the "Galathea" section was found to vary between 95 and 120 m., with the exception of the stations near the Equator, where a depth between 78 and 85 m. was found. The layer was 77 m. deep at Station 700. The latter station is in the approaches to the Californian coast.

No straight dependence of the rate of production on the concentration of phosphate is seen in the tropical part of the section in question. *A priori* this is not to be absolutely expected – cf. p. 93, where the influence of phosphate is discussed. Thus at Station 692 near the Equator where the phosphate concentration at all depths of the photosynthetic layer was 0.7 μg-atom P/l. a much higher rate than observed, 0.14 g. C/m.^{2}/day, could have been expected. Certainly the high phosphate-concentration may not have been accompanied by equally high nitrate-concentrations. Available N was very likely the real limiting factor for organic production. As will be shown in Fig. 28, p. 93 the surface water of the South Equatorial Current about the longitude in question, according to the "Dana" observations showed a characteristic minimum in nitrate whereas phosphate was relatively abundant.

The effect of a divergence on the plankton production is, in all probability, not restricted to the precise location of the divergence. Through the horizontal currents a bigger area is positively affected. Without the help of really extensive observations, an area like the equatorial region of the Pacific cannot be treated in much detail.

The section from San Francisco to Panama along the American coast will only briefly be presented. All stations were located in water either very productive or at least rather productive. It is to be expected that an extensive series of observations from all seasons will be available in the near future through productivity work made at the Scripps Institution of Oceanography. It would thus be premature to try to use the present scant data for any detailed study.

Besides Station 420 in the Golf at Panama, where the rate of production was measured in the normal way in water from 3 different depths, determinations of the production in surface water samples were made at two other stations, giving a rate somewhat less than at Station 420.

E. THE PRODUCTION OF ORGANIC MATTER IN THE HYDROSPHERE AS A WHOLE

Investigations on a much greater scale than was possible during a single circumnavigation of the globe are of course needed to get exact figures for the production of matter in the seas.

In previous publications – Steemann Nielsen 1952 and 1954 – the senior author has estimated the average annual gross production of matter in all seas to be 55 g. C/m.^{2}. This estimate is perhaps a little too low. The rate of production in antarctic waters was perhaps a little underestimated. No observations at all are available. The average annual gross production for all seas exceeds, however, hardly 70 g. C/m.^{2}. If we use a value of 55-70 g. C/m.^{2} and reckon on a 40 per cent. loss through respiration (my previous figure, 25 per cent., is presumably too small) and a sea area of 361 × 10^6 sq. km., we obtain a total net production per year in the sea of 1.2-1.5 × 10^{10} tons of carbon. This figure is practically the same as that estimated by Schroeder 1919 for the production on land. Before many more observations are available it is pointless to try to obtain a better estimate of the production of matter in the hydrosphere. Investigations carried out during the "Galathea" Expedition have shown that the amount of organic production in the tropical and subtropical parts of the oceans is strictly dependent on the hydrographic conditions. Although experiments were made only once at each station there is every indication that the results obtained in the main provide a reasonably correct picture of the productivity of the region. It must of course be stressed that this is by no means applicable to temperate and arctic waters, and only partly to some tropical and subtropical waters.

It is possible to distinguish four different classes of oceanic regions according to amounts of organic production. These are applicable only to tropical and subtropical parts of the oceans. Graduations between them are found of course.

(I) Regions with a very considerable admixture of "new" water to the photosynthetic zone. "New" water is water rich in nutrient salts originating from medium depth. The daily organic production is from 0.5 to about 3 g. C per square metre. An example of this class is the southern part of the Benguela Current.

(II) Regions with a fairly steady admixture of "new" water to the photosynthetic zone. The daily organic production is about 0.2-0.5 g. C per square metre. This may be exemplified by the regions in the neighbourhood of the divergences caused by the Equatorial Counter-Currents in the different oceans.

(III) Areas without a pronounced admixture of nutrient-rich water from below. Some admixture –

although of minor importance – may occur, however, through turbulence. The daily organic production is 0.1-0.2 g. C per square metre. By far the largest parts of the tropical and subtropical regions of the oceans belong to this category.

(IV) Areas with typically "old" surface water in the photosynthetic zone. This water, originally rich in nutrients, has been transported from a distant region, and the lapse of a long time has resulted in decrease in nutrient content since the water entered the photosynthetic layer. Turbulence is of only slight importance, since nutrient-rich water is present only far below the photosynthetic zone. The rate of organic production is about 0.05 g. C per square metre per day. An example of this is the central part of the Sargasso Sea.

As a general rule it may be stated that the organic production is high in the shallow coastal regions of the Tropics. It may be supposed that the high temperature of the bottom material during the whole year gives rise to a fast decomposition rate of organic material producing considerable amounts of the nutrient salts – cf. p. 86.

According to the Fishery statistics (F.A.O.) the annual yield of all of the marine fisheries is at present 2.4×10^7 tons of fresh weight. If this is converted into carbon it indicates that about 0.01 per cent. of the carbon annually fixed in the plankton algae in all seas is taken every year by the fishermen.

0.01 per cent. does not seem to be very much. But it must be kept in mind that fishing is not going on at all in most parts of the oceans. Unfortunately fishing in many of these areas will hardly ever be economically possible.

In eutrophic coastal areas at higher latitudes – as e.g. the North Sea – about 0.2-0.3 per cent. of the carbon annually fixed by the plankton algae is taken every year by the fishermen. There is every indication that such a high percentage of the yield is possible only in eutrophic areas where further a material part of the fish caught is represented by species like the herring. Mostly only one link is found in the food chain between plankton algae and herring. The problems will be discussed in detail in another publication dealing with the recent Danish investigations on production of organic matter in the northern seas.

PART III.
THE GENERAL BACKGROUND OF OCEANIC PRODUCTIVITY

A. INTRODUCTION

It is now rather well established (see e.g. Sverdrup *et al.*, 1942) that the main factors governing the production of phytoplankton in the sea are the following: A) the supply of nutrient salts, B) light, C) temperature, D) sinking, E) grazing by animals. Other factors like hormones and antibiotics produced by the phytoplankton itself or by other organisms are undoubtedly also of importance. At present, however, we know little about the effects of such factors in the open ocean. Lucas 1947 discussed the whole matter. It is very likely that external metabolites have at least some influence on the production rate of phytoplankton even in the open ocean – cf. p. 114.

The investigations made on the "Galathea" Expedition have furnished considerable evidence that the supply of nutrients – manifested by the "age" of the surface water in the sense used by Sverdrup and Allen 1939 – is by far the most important factor governing the production of phytoplankton in the tropical and subtropical parts of the oceans. Subsurface water recently ascended to the surface is called "new". The concentrations of the nutrient salts are high in such water. In "old" surface water the nutrient salts are exhausted due to the activity of the plankton algae.

Nature has normally established an equilibrium between all the factors governing phytoplankton production; it is only occasionally possible at any given time to describe one of the factors as the absolutely limiting one. Any change in one of the factors mentioned above will normally influence the other factors as well and establish a new equilibrium. All of these factors should therefore be treated as inseparable. However, in the interest of clarity in this chapter, only attempts in this direction will be made in the main sections; in conclusion a comprehensive survey of the whole complex will be given.

B. SUPPLY OF NUTRIENT SALTS

1. Nitrate versus Phosphate

The two elements nitrogen and phosphorus often become limiting for the production of organic matter in the oceans. In oceanic water it seems never to have been definitively stated that other elements such as iron may act in the same way. A survey of these problems may be found in Sverdrup *et al.* 1942.

Whereas inorganic phosphate is easily determined, it is not quite so with the inorganic nitrogen sources which are assimilated by plankton algae. In coastal water the difficulties are particularly great, since both ammonia, nitrite and nitrate may be found in nearly equally important quantities – cf. Steemann Nielsen 1951. The determination of nitrate in coastal water was till recently often inexact. The reduced strychnine method, originally introduced by Harvey 1928, may be inadequate in productive water of that kind.

In the open ocean, the difficulties are much fewer. According to the experiences obtained during the "Dana" Expedition 1928-1930, the reduced strychnine method seems to give reasonably reliable measurements of nitrate in oceanic water having a normal content of plankton. In very plankton-rich water it may be different.

In recent years only the concentration of phosphate has been measured in most investigations – for example during the "Galathea" Expedition, where the determinations were made according to Wattenberg 1937 and corrected for salt error according to Cooper 1938.

Apparently there seems to be good reason for determining only phosphate. According to Redfield 1934, the ratio of phosphorus as inorganic phosphate to nitrogen as nitrate is nearly constant in the oceans. In the Atlantic he found essentially a constant ratio down to the smallest concentrations of both elements; thus these should be exhausted simultaneously due to the activity of the plankton algae.

Cooper 1937, 1938, has also discussed the N: P ratio in the sea. In principle he agrees with Redfield. He gives (1938) an "ideal" ratio of 15 when the concentrations are expressed as µg-atom/l. and the phosphate determinations are corrected for salt error. He showed, however, that anomalies in the

N: P ratio may be found. In oligotrophic areas of the Mediterranean the ratio was much above the "ideal" value. He used the phosphate and nitrate observations made during the "Dana" Expedition 1928-1930 in the Mediterranean to prove this statement. These observations were published by THOMSEN 1931. In the same paper some scattered observations from the Atlantic, the Pacific and the Indian Ocean were published out of the great number of observations made during the expedition. REDFIELD 1934 made use of these few published observations.

HARVEY 1945 noted that the N: P ratio was abnormally low in certain waters of the South Atlantic. He suggested that it may be due to the direct regeneration of phosphate being more rapid than the indirect regeneration of nitrate in such water. RILEY *et. al.* 1949 p. 18 refer to the same suggestion but mention in addition, that "it might also be implied that nitrogen is the more important limiting factor, particularly in the southern areas".

THOMSEN 1937 has published the entire observations from the "Dana" Expedition 1928-1930, unfortunately, however, without any accompanying text. Some characteristic features from this valuable collection of observations will be presented here. No attempt will be made to treat these numerous observations in detail. In Part II some of the "Dana" observations have already been used. The phosphate determinations have been corrected for salt error according to COOPER 1938.

Whereas a N: P ratio of about 15, as given by Cooper, is adequate for the Northern Atlantic, the ratio seems to be smaller in most other parts of the oceans. This is also the case in deep water, where it mostly is about 12-14. Particularly low ratios are found in the eastern part of the South Pacific. The "Dana" Station 3563 may be used as an example – Table 7.

Table 7. Nitrate and Phosphate at "Dana" Station 3563 7°45'S, 131°22'W. 29. 9. 1928.

depth in m.	μg-atom $N\text{-}NO_3$/l.	μg-atom $P\text{-}PO_4$/l.	N:P
0-50	2.8	0.5	5.6
75-100	2.8	0.6	4.8
150	3.6	0.6	6.0
200	10.7	1.1	9.8
300	19.6	1.7	11.5
400	19.6	1.7	11.5
500	25.0	2.4	10.5
600	28.6	2.4	11.9
1.000	26.8	2.9	9.3
1.500	26.8	3.0	9.0
2.000	28.6	2.9	9.9
3.000	28.6	2.4	11.9
4.000	28.6	2.4	11.9
4.500	26.8	2.4	11.2

The concentrations of both nitrate and phosphate were sufficiently high at all depths to allow the compution of a fairly exact: N: P ratio. The highest ratio found at any depth was 11.9. On the average it was definitely lower. The very low ratios varying between 4.8 and 6.0, found in the water layers between the surface and 150 m. are of special interest in this connection.

Let us suppose that deep water from "Dana" Station 3558 originally was brought up into the photosynthetic layer. Station 3558 was the most eastern station in the South Equatorial Current situated near a centre of real upwelling (0°18'S, 99°07'W). The nitrate concentration in this deep water was 35.7 μg-atom N/l., the phosphate concentration was 3.0 μg-atom P/l. The plankton algae have now assimilated both nitrate and phosphate during the westward drift of the surface water. According to determinations by Fleming cited in SVERDRUP *et. al.* 1942 p. 236, the ratio of N: P in plankton diatoms may be put at 16, in good agreement with the ratios presented by REDFIELD 1934 and COOPER 1937. If therefore the nitrate concentration due to the assimilation by the phytoplankton is reduced to 2.8 μg-atom/l. (the actual concentration found in the photosynthetic layer at Station 3563), 32.9 μg-atom/l. is thus assimilated; if the ratio assimilated N: assimilated P is put at 16, 1.9 μg-atom P/l. is thus consumed, leaving 0.9 μg-atom in the water. This is in good agreement with the 0.5 μg-atom P actually found in the surface layer 0-50 m. at Station 3563. The low N: P ratios near the surface are thus easy to explain.

If all the nitrate had been assimilated, theoretically we should still have expected about 0.8 μg-atom P/l. In order to demonstrate the decrease in the N: P ratio, the nitrate and phosphate concentrations near the surface (0-50 m.) from a section of the "Dana" following the South Equatorial Current in the South Pacific from the Galapagos Islands to north of New Zealand are presented. The N: P ratio found is also given and finally the theoretical ratio is presented. The latter was derived on the assumption that the $N\text{-}NO_3$ and $P\text{-}PO_4$ concentrations prior to any assimilation by the plankton algae were 35.7 and 3.0 μg-atom/l. respectively (the values at Station 3558 in the deep water).

Table 8. The average concentrations of N-NO_3 and P-PO_4 and the actual and "theoretical" N:P ratio in the uppermost 50 m. of the South Equatorial Current in the Pacific. Observations at depths of 0, 10, 25 and 50 m.

Station No.	Position	μg-atom N-NO_3/l.	μg-atom P-PO_4/l.	actual ratio N:P	"theoretical" ratio N:P
3558	0°18′S-99°07′W	11.6	1.25	9.3	7.8
3561	4°20′S-116°46′W	5.7	0.85	6.7	5.2
3563	7°46′S-131°22′W	2.8	0.5	5.6	3.1
3573	17°36′S-149°42′W	0.1	0.6	(0.2)	0.1
3577	18°49′S-153°10′W	0	0.2	–	–
3580	18°53′S-163°02′W	0.1	0.2	(0.5)	0.1
3624	28°17′S-177°01′W	0	0	–	–
3626	27°00′S-177°41′W	0	0	–	–

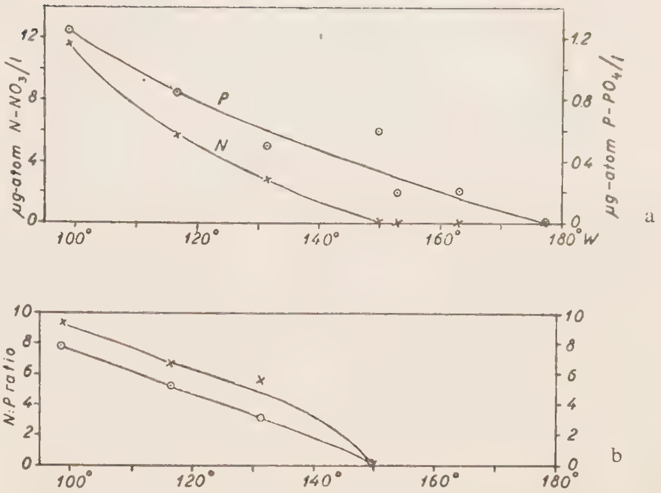

Fig. 28a and b. The observations and calculations given in Table 8 are graphically presented.

In Fig. 28a and b, the observations and calcualtions are presented graphically. In the whole section the actual and the "theoretical" ratios agree very well. In the South Equatorial Current in the Pacific about 150°W, relatively high concentrations of phosphate are found although nitrate is almost completely exhausted. During the "Galathea" Expedition, a section was made across the current at approximately this longitude. The relatively high phosphate concentrations found in the photosynthetic layer at Stations 691 and 692, Table 20, may thus not neccessarily be a symptom of excellent growing conditions for the plankton algae. The relatively low rates of organic production found in this region may thus be explained.

The facts presented are a memento; it may sometimes be wrong to assume that excellent nutrient conditions follow from relatively high phosphate concentrations if determinations of this nutrient only have been made.

As shown above, the low N: P ratios in the photosynthetic layer of the South Equatorial Current in the Pacific was ascribed to the relatively low ratio in the deepwater ascending to the surface in the easternmost part of the current. As the ratio assimilated N: assimilated P was definitely higher, the ratio present N: present P decreased when the concentrations of the nutrient decreased.

Table 9. The average concentrations of N-NO_3 and P-PO_4 and the N:P ratio off the Atlantic coast of North Africa. Observations at depths of 0, 10 and 25 m.

Station No.	Position	μg-atom N-NO_3/l.	μg-atom P-PO_4/l.	N:P
4007	18°22′N-18°14′W	10.1	0.9	11.3
4005	13°31′N-18°03′W	7.0	0.6	11.7
4003	8°26′N-15°11′W	4.8	0.5	9.6

In the eastern part of the North Atlantic off the coast of North Africa a similar upwelling of deep water occurs. The N: P ratio in this water of about 15 – Cooper's ideal ratio – has the effect that the ratio decreases only slightly when the nutrient salts are assimilated by the phytoplankton. Table 9 which gives the nitrate – and phosphate concentrations and the N: P ratio in the uppermost 25 m. at three representative "Dana" stations, shows this clearly.

Other comments on the N:P ratio in oceanic water may be made. As shown in Table 8, both nitrate and phosphate are fully exhausted in the photosynthetic layer at the last two stations of the section along the South Equatorial Current in the Pacific – Stations 3624 and 3526. It could be supposed that this situation was caused by a high N: P ratio for "new" surface water. The surface water at these stations should hence originate not in the more eastern part of the current, but should consist mainly of water from deeper levels at the location. This water originally should have had a high N:P ratio. The N:P ratio in the subsurface water at these stations is, however, by no means high – Table 10.

We are thus forced to assume that when surface water, in which nitrate is fully exhausted but phosphate is not, becomes still "older", it also becomes exhausted with respect to phosphate. This may be explained in several ways, as e.g., by a faster regeneration rate of nitrate (including ammonia and

Table 10. Nitrate and phosphate at "Dana" Station 3626-27°00'S, 177°41'W.

Depth in m.	µg-atom N-NO$_3$/l.	µg-atom P-PO$_4$/l.	N: P
0-50	0	0	–
65-100	0.1	0.15	(0.7)
200	1.4	0.3	4.7
300	3.6	0.4	9.0
400	7.1	0.6	11.9
500	10.7	0.9	11.9
1.000	26.8	2.2	12.2
2.000	39.2	2.9	13.5

Table 12. Nitrate and phosphate at "Dana" Station 3542 – 24°52'N, 44°40'W.

Depth in m.	µg-atom N-NO$_3$/l.	µg-atom P-PO$_4$/l.	N: P
0-100	0.1	0	–
150	0.3	0	–
200	2.5	0.15	17
400	11.7	0.3	39
600	23.2	0.5	47
800	25.0	0.85	29
1.200	26.8	0.65	41
1.500	23.3	0.55	42

nitrite) in the photosynthetic layer or by addition of nitrate from rainwater or by assimilation of elementary nitrogen by blue-green algae. No marine plankton species having this ability are known, however.

The supply of nitrate in rainwater due to electrical fixation in the atmosphere is hardly of any decisive importance for the entire photosynthetic layer. Even if, according to Benecke-Jost 1924, we take the greatest supply found in the Tropics – 0.6 g N-NO$_3$/m.^{2}/year – this would correspond only to 0.09 g. P-PO$_4$/m.^{2}. If the photosynthetic layer is 100 m. deep, it would further correspond only to 0.9 mg. P/m.^{3} = 0.03 µg-atom P-PO$_4$/l.

For the actual surface on the other hand, the nitrate from rainwater may be of some importance. A high percentage of the "Dana" stations in the parts of the oceans (primarily the Indian Ocean), where nitrate was found to be lacking in the photosynthetic layer, but where phosphate was still present, showed an absolute phosphate depletion in the actual surface; on the other hand, small concentrations of nitrate sometimes were found there. The contribution of nitrate to the actual surface makes it possible for the algae to utilize the remaining quantity of phosphate. The "Dana" Station 3850, Table 11 presents a typical example.

Table 11. Vertical distribution of N-NO$_3$ and P-PO$_4$ at "Dana" Station 3850. 6°01'S, 93°12'E.

depth in m.	µg-atom N-NO$_3$/l.	µg-atom P-PO$_4$/l.
0	0.1	0
10	0	0.2
25	0	0.2
50	0	0.2
75	0	0.2
100	14	1.0

If nitrate is regenerated faster than phosphate, we must expect a high N: P ratio in the water masses just beneath the photosynthetic layer in areas of descending surface water. Nitrate and phosphate found here must originate chiefly from organic matter produced in the surface layers. Such areas are mostly extremely oligotrophic. Using the "Dana" observations, Cooper 1937 has already shown that such conditions are found in the eastern Mediterranean, where just such a descent of surface water takes place. A similar area is found in the North-Atlantic eddy- the Sargasso Sea. Riley *et. al.* Fig. 8 presented the vertical distribution of the ratio at a station from the northwestern border of this area. In Table 12, the vertical distribution of the concentrations of nitrate and phosphate are presented together with the ratio from a "Dana" station located in the centre of the Sargasso Sea where particularly high ratios are found.

It may be supposed that the regeneration rate of nitrate probably mostly is faster than that of phosphate. In quite "new" surface water, the amounts of the salts regenerated may be considered to be relatively small compared to the primary amounts present. They are thus of little importance for the N:P ratio. When the original nitrate is used the regeneration rate becomes important. In the long run, the greater amounts of nitrate regenerated in the photosynthetic layer cause all the phosphate to be used by the plankton algae. In very "old" surface water both nitrate and phosphate are thus exhausted.

It was shown above that in areas where surface water descends, the N: P ratio in the water layers immediately below the photosynthetic layer has a very high N:P ratio. According to the "Dana" observations positive anomalies were also found just beneath the photosynthetic layer near the divergence at the northern boundary of the South Equatorial Current in the Indian Ocean. A N:P ratio

Table 13. Nitrate and phosphate at "Dana" Station 3925 – 7°13'S, 52°22'E.

Depth in m.	μg-atom N-NO_3/l.	μg-atom P-PO_4/l.	N:P
0	0.3	0.1	–
10	0	0.2	–
25	2.1	0.5	4.2
50	16.1	0.75	21.4
75	23.2	1.15	20.1
100	28.5	1.15	24.8
150	30.4	1.6	19.0
200	30.4	1.7	17.8
400	30.4	2.1	14.5
1.000	43.0	3.15	13.7
2.000	43.0	3.15	13.7

of 20.6 was found at a depth of 150 m. at "Dana" Station 3848 of the section 4 – cf. Fig. 24 and p. 84 The "Dana" Station 3925 from the section 2, Fig. 24 gives the best illustration, Table 13. "Dana" Station 3585 located about 450 miles south of the corresponding divergence in the Pacific (but about 100 miles north of the "Dana" section presented in Fig. 25, p. 83) had a N:P ratio of 19 and 21 in depths of 400 and 500 m. respectively.

It seems at present impossible to give any absolutely convincing explanation of the high N:P ratio found at depths between 50 and 200 m. in these particular areas. It is perhaps an indication of an especially high regeneration rate of the nutrient salts at these depths. Such high N: P ratios are rarely found below the photosynthetic layer in eutrophic regions.

It is rather obvious however, that differences may be expected between the various regions. A quantitative knowledge of all of the processes going on would be necessary for a real understanding. We do not by far possess such a knowledge today.

Whether nitrogen or phosphorus is the real limiting factor for the organic production varies from area to area. At present it is possible to say that generally speaking nitrogen is the most important limiting factor in areas where the replenishment of the nutrients is due particularly to a supply originally brought up near the surface by subsurface water. In areas in which the replenishment is due primarily to a direct regeneration, either in the water of the photosynthetic layer or at the bottom in contact with this layer, phosphorus particularly becomes limiting – cf. the conditions in the Danish Isefjord, STEEMANN NIELSEN 1951.

2. The replenishment of nutrients

As clearly pointed out for example by KETCHUM 1947, "it is the rate of replenishment, and not the concentration observed at a given time, which determines the fertility of an aquatic environment. This replenishment is provided by the two processes of decomposition and water circulation."

Neither of these processes is too well known – the best, however, being the water circulation. The nutrient salts are brought into the photosynthetic layer by turbulence, including eddy diffusion, and by upwelling. The latter requires special hydrographic conditions. It is therefore found only at special places – as in the South Atlantic near the coast of Africa. As subsurface water containing a relatively high concentration of the nutrient salts is transported up to the surface during upwelling, the influence of this process is very pronounced on the replenishment of the nutrients and thus on the organic productivity.

The influence of turbulence is less than upwelling on the one hand. On the other, it is of a more universal occurrence. Whereas turbulence may be investigated quantitatively in some waters without great difficulty (see JENSEN 1940), the problem seems at present to be rather difficult to handle in most oceanic areas. Turbulence, as will be used in the present section, may be described as the process by which the photosynthetic layer interchanges water masses with the layers just below it. It is therefore of immense importance for the transport of nutrient salts, how the concentrations of these are in the water layers just below the lower boundary of the photosynthetic zone.

The concentration of inorganic phosphate at a depth of say, 50 m. below the lower boundary of the photosynthetic zone may therefore often provide a usefue indication of the influence of turbulence on the transport of the nutrient salts into the photosynthetic layer. Although phosphate determinations below the photosynthetic zone were only sporadically made on the "Galathea", sufficient material is available from other expeditions for most of the areas investigated. The degree of stability of the water masses must be assumed to have a comparably strong influence on the transport of the nutrient salts into the photosynthetic layer. It is therefore not possible to use the concentration of nutrients just below the photosynthetic layer as an index of potential nutrient supply without reservations.

At present it is possible to investigate only indirectly the problem of the regeneration of the inorganic phosphate from soluble organic phosphate and from particulate, "dead" phosphate. The same is the case with nitrogen. Because of the enormous development of bacteria on bottling a sample of natural water no experimental investigation of regeneration under natural conditions seems possible at present.

The regeneration of e.g., phosphate could be measured indirectly by investigating the rate of photosynthesis if sufficient knowledge of the importance of vertical mixing of the water masses were available. It may be supposed that roughly 1 mg. P is assimilated for every 40-50 mg. C – cf. e.g. Redfield 1934. In one of the least productive areas of the oceans – the Sargasso Sea – the rate of photosynthesies is about 0.5 mg. C per m.^{3} per day near the surface – cf. Table 20. The rate of phosphate assimilitation may thus be estimated to be about 0.01 mg. P per m.^{3} per day. This is apparently about 1 per cent. of the concentration of inorganic phosphate normally found here – cf. Table 20.

As fairly phosphate-rich water in the Sargasso Sea first is found several hundred meters below the photosynthetic zone (cf. Table 12), and as the water masses show a tendency of descending, turbulence must be assumed to be of very little importance here for the phosphate replenishment in the photosynthetic zone. Assuming stable conditions, the daily regeneration rate of inorganic P may thus be estimated to be about 0.01 mg. P/m.^{3}.

For comparison, another marine area may be mentioned where the same phosphate concentration as in the Sargasso Sea was found during a period of the summer. During 3 series of investigations in the very productive Danish Isefjord (Steemann Nielsen 1951) in the period August-September 1941, the phosphate concentration (inorganic) was about 1 mg. P per m.^{3} The organic productivity in this period varied between 250 and 520 mg. C per m^3. per day at the surface. P-assimilation may thus be estimated to be about 5-10 mg. per m.^{3} per day. The amount assimilated daily is thus about 5 times the amount present at any given time. It may therefore be stated that the inorganic phosphate present in solution at any moment in a water mass may represent from 1 to 500 per cent of the amount taking part in the daily metabolism. According to all evidence available inorganic phosphate must be assumed to be present in greater quantities than those indicated by the determinations of phosphate in solution. At the low P-concentrations found in Nature, a relatively considerable adsorption of phosphate must be expected to take place at all surfaces – for example at the surfaces of detritus. As the phosphate in solution must be in equilibrium with the phosphate adsorbed, the latter may very likely often represent an important P-reserve.

Paradoxically the phosphate supply apparently seems to be most secure for the algae in the oligotrophic water from the Sargasso Sea where the amount of inorganic phosphate in solution present at any moment is sufficient for the normal consumption during a long period. It could be supposed that the few algae present here hardly ever suffer a really pronounced phosphate deficiency. This is true in spite of the fact that the scarcity of algae and the low rate of organic productivity found is caused ultimately by poverty in phosphate and other nutrients. This puzzling problem is discussed further on p. 113.

In the shallow Danish fjord where the water masses are without stratification and are in constant contact with the bottom, the regeneration of the nutrient salts – presumably taking place primarily at the surface of the bottom deposits – represents virtually the only way in which the nutrients are supplied. The dependence of organic productivity on temperature – cf. Steemann Nielsen 1951 – indicates that this factor affects the regeneration of the nutrient salts very pronouncedly.

In open waters quite another picture is obtained. Ketchum 1947 discusses the problem in a very instructive article. He deals with the Gulf of Maine. The total assimilation of phosphate during the production period is calculated as 8 g. PO_4 (= 2.7 g. P) per m.^{2}. Of this, only 2 % originated from the inorganic phosphate originally present in the photosynthetic layer, 73 % was brought to the surface by vertical transport and – "estimated on meager grounds" as Ketchum states – 25 % was supplied by decomposition within the surface layer. The calculated daily total utilization of 14 mg. P per m.^{2} per day corresponds to 560 mg. assimilated C per m.^{2}, a production rate to be expected during the summer season in the Gulf of Marine.

It is unfortunately rather improbable that the conceptions concerning regeneration of inorganic phosphate in coastal waters and in freshwater lakes can be directly used for marine areas of another kind. Not even a knowledge of the concentration of organic phosphate and of detritus containing P would necessarily give any real information about the rate at which inorganic phosphate may be regenerated at a certain temperature.[1] Soluble organic phosphates may be of a different nature; some easily accessible for attack, some not so easily. It is possible that in "new" surface water a higher proportion of both the soluble organic phosphate and the P in the detritus (besides the adsorbed phosphate) may be relatively rapidly regenerated into inorganic phosphate, whereas in "old" surface water an accumulation has taken place of material more difficult to decompose. It seems very likely that the regeneration of the nutrient salts takes place rather slowly in the water masses of the photosynthetic layer, at least in ologiotrophic oceanic areas. The same seems to be the case in the water masses below the photosynthetic layer. At the two "Dana" stations in the Sargasso Sea – 3543 and 3545 – at a depth of 200 m. – i.e. about 100 m. below the compensation depth – a phosphate concentration of only 0.1 mg.-atom P/m.^{3} was found. As the consumption of phosphate must be supposed to be zero at this depth the rate of regeneration is low.

It is usually assumed that the demineralization of the salts containing N and P is due to the activity of bacteria. This is true concerning the sea bottom according to all evidence.

The mineralization occuring in the free water masses on the other hand may be due not predominantly to the activity of bacteria, but to enzymes found in the water. Because of antibiotics produced by the phytoplankton in light, the activity of most species of bacteria seems to be rather restricted near the surface – STEEMANN NIELSEN 1955b.

KREPS 1934 has presented weighty evidence that enzymes catalyse chemical reactions such as NO_3-production in samples of sea water, poisoned with $HgCl_2$, or filtered through an ultrafilter. The enzymes have their origin in plants, animals or bacteria and they are presumably released in the water due to the death of the organism.

Kreps writes: "It is highly probable that bottom deposits and bottom water layers, which contain most of the organic matter originating from dead animals and plants, planktonic as well as bottom living, are especially rich in various enzymes increasing the rate of various chemical reactions. Liberated in the bottom strata, these enzymes may be involved in the vertical mixing, and are so brought up in the whole water mass, exerting everywhere their catalytic action".

In oceanic surface water enzymes may presumably also be liberated into the water particularly from algae, which have been eaten by the zooplankton. It must, however, be supposed that the concentration of these enzymes is very low in oligotrophic oceanic surface water. This would be in accordance with the apparently slow rate of P- and N-regeneration in such areas.

The hydrolysis of most of the phosphorylated organic compounds is very likely proceeding at a measurable speed without the presence of enzymes. Inconsiderable enzyme concentration should thus be sufficient to account for the rather slow rate of regeneration of inorganic phosphate from soluble organic phosphate found in oceanic water.

3. Concentration of nutrients and rate of organic production in the different oceans

It is at present impossible to compare the rates of organic production in the different oceans. The available data are too few and too scattered. In broad outline, the different oceans do not seem to vary much in this respect. Some differences may, however, be expected.

The distribution of nitrate and phosphate is at least an indication of a possible difference in organic

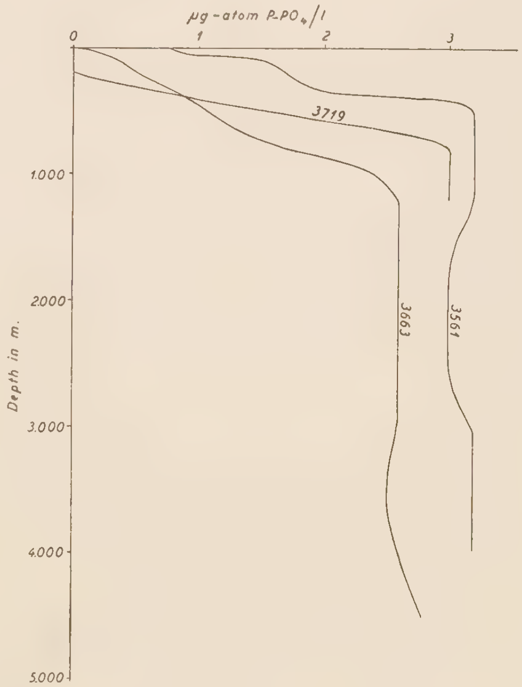

Fig. 29. The vertical distribution of phosphate (μg-atom P/1) at three Dana stations in the Pacific Ocean. St. 3561 – 4°20'S, 116°46'W. St. 3663 – 33°33'S, 154°04'E. St. 3719 – 20°48'N., 124°49'E.

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[1] The procedure of measuring total phosphorus in surface waters such as stressed by KETCHUM *et. al.* 1955 must, however, be considered an important improvement.

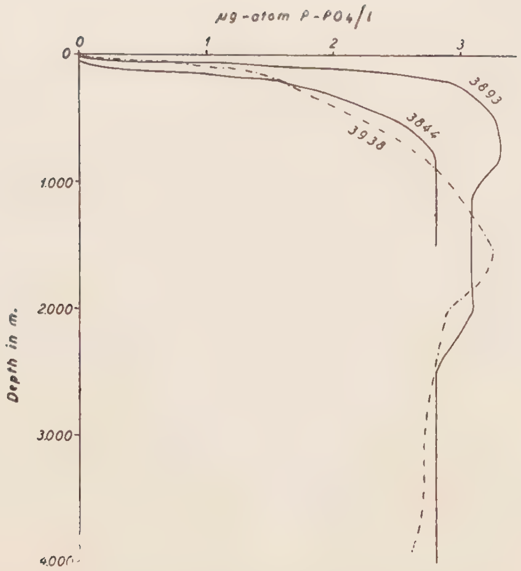

Fig. 30. The vertical distribution of phosphate (μg-atom P/l) at three Dana stations in the Indian Ocean. St. 3841 – 12°05′ S., 96°44′E. St. 3893 – 5°59′N., 92°29′E. St. 3938 – 9°10′S., 45°17′E.

production. According to the distribution of these salts the North Atlantic could be expected to be somewhat less productive than the oceans in general. On the average the water masses particularly of the North Atlantic but also of the South Atlantic contain less phosphate and nitrate than the oceans in general. This fact is well known – cf. Sverdrup *et. al.* 1942.

In Fig. 29-31 the vertical distribution of phosphate is presented for three representative stations in each ocean. The data originate from the "Dana" – Thomsen 1937.[1] Whereas all stations from the Pacific and the Indian Ocean are generally similar the stations from the Atlantic give quite another picture if the upper water masses are disregarded.

Station 3998 from the eastern part of the South Atlantic resembles (for the water-layer from the depths about 200-1,000 m.) Station 3561 from the eastern part of the South Pacific or Station 3893 from the eastern part of the Indian Ocean. The maximum P-concentration in the Atlantic at these depths is 3.0 μg-atom P/l. and 3.2-3.3 in the Indian Ocean and the Pacific respectively. Below a depth of about 1,000 m., at the Atlantic station, deep water is found showing a P-concentration of about 1.8 μg-atom/l. In the deep water found at the two stations in the other oceans, the P-concentration is about 3.0 μg-atom/l. The origin of the water masses found in the South Atlantic Ocean – a survey is given by Sverdrup *et. al.* 1942 p. 625 ff. – explains the vertical distribution of phosphate.

At Station 3998 the intermediate water rich in phosphate is of Antarctic origin, whereas the deep water with the exception of a thin bottom layer-originates from higher latitudes on the Northern hemisphere.

According to Sverdrup *et. al.* Table 76 the following water masses are transported across the equator towards the north: 6×10^6 m.^{3}/sec. upper water, 2×10^6 m.^{3}/sec. intermediate water and 10^6 m.^{3}/sec. bottom water. In the southerly direction, 9×10^6 m.^{3}/sec. deep water are transported. The amounts of nutrient salts being transported in either direction must be the same. If the average P-concentration of the deep water is put at 1.8 μg-atom/l., 16 kg. P/sec. are transported northwards. If the P-concentration in the intermediate water is put at 3.0, and that in

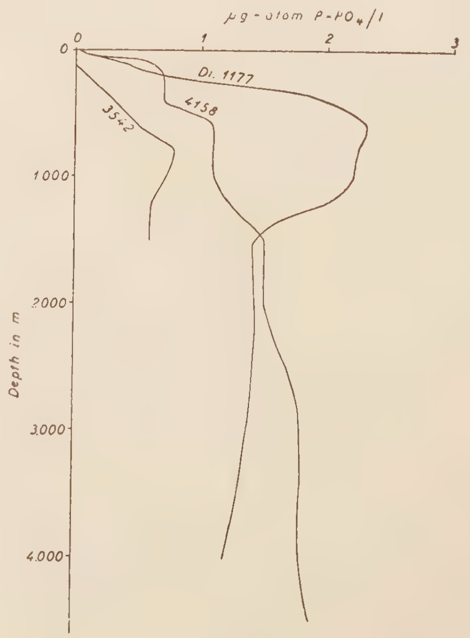

Fig. 31. The distribution of phosphate (μg-atom P/l) at three stations in the Atlantic Ocean. St. Discovery 1177 – 19°S., 1°30′W. St. Dana 4158 – 46°28′N., 8°01′W St. Dana 3542 – 24°52′N., 44°40′W.

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[1] The curve for the South Atlantic originates, however, from the "Discovery" – Clowes 1937. Whereas for all other areas of the oceans the P-observations from the "Dana" agree very well with observations obtained during other expeditions, this is not so in the South Atlantic.

The "Dana" observations are about 35 per cent. higher than the "Discovery" observations (both corrected for salt error). Unpublished observations from the "Meteor" kindly provided by Professor J. Krey, Kiel – agree with the "Discovery" observations. It is only possible now to guess about the failure of the "Dana" in the South Atlantic. During the section northwards from Cape Town, the wrong determinations seem first to start at St. 3980 (23°26′ S, 3°56′E). At St. 3978 (30°15′S, 13°15′E), the "Dana" and the "Meteor" observations agree.

the bottom water at 2.0 μg-atom/l., $6+2 = 8$ kg. P/sec. is transported northwards by these water masses. 8 kg. P/sec. must thus be transported by the upper water. This means that the P-concentration must be 1.3 μg-atom/l. on the average. The real concentration of dissolved inorganic phosphate is decidedly lower. In making a computation of the present kind we have, however, to use the values for total P. Particulate P and dissolved organic P must be included. An average concentration of about 1.3 μg-atom total P/l. seems rather likely for the upper water. In the other water masses, practically all of the P is in the form of inorganic phosphate in solution.

Because the total amount of inorganic P below a surface unit in the North Atlantic Ocean is only about 50 per cent of that in the other oceans, this does not necessarily mean that the amount of P annually used by the phytoplankton below a surface unit is much lower in the North Atlantic than elsewhere on the average. Other instances are also of importance. In the North Atlantic including the Arctic waters, it may thus be stated that in broad outline all phosphate conveyed up into the photosynthetic layer is used by the algae. This is in contrast to the conditions in the Antarctic Ocean. The high concentrations of phosphate and nitrate found at all seasons in these waters indicate that some factors – chiefly the lack of an effective stabilization of the water masses – do not allow the nutrients to be fully utilized.

The Mediterranean presents an example of a reduction in the amount of nutrients of quite another order of magnitude compared to the North Atlantic Ocean. In the eastern part of the Mediterranean only about 7 per cent. of the phosphate normally found in the oceans (depth 0-4,000 m.) was measured by the "Dana" – THOMSEN 1937. According to the quantitative zooplankton investigations – JESPERSEN 1935, the eastern part of the Mediterranean is extremely poor in plankton. If the productivity of the North Atlantic is influenced by the reduced amounts of phosphate found in the watermasses as a whole, this reduction must be assumed to be rather limited.

4. Experiments with ocean water to which nutrient salts are added

It is a well known fact that it is possible to increase the growth of phytoplankton in a sample of coastal water enclosed in clear glass bottles and exposed to light, if the concentrations of the nutrient salts are increased. This procedure seems, however, not to be possible in true oceanic water. HENTSCHEL 1932 refers to such experiments made on the "Meteor" Expedition.

Table 14 (after HENTSCHEL 1932).

	Initial count, bottle a	Initial count, bottle b	Count after 26 hours, bottle c, phosphate added	Count after 26 hours, bottle d, no phosphate added	Count after $37^1/_2$ hours, bottle e, phosphate added
diatoms	244	237	132	99	6
coccolithophorides	672	938	249	165	66
dinoflagellates	996	1405	297	650	369

At the "Meteor" Station 254 in the Southern Atlantic near the Equator, surface water was enclosed in 2 litres bottles which were suspended near the surface for either 26 or $37^1/_2$ hours. Phosphate was added in 2 bottles but not in a third. The plankton was counted at the start of the experiment and after 26 and $37^1/_2$ hours. Table 14 shows the results.

It is obvious that the plankton cannot tolerate enclosure in the glass bottles for 26-37 hours. Under these circumstances it is impossible to see any effect of added phosphate. During the "Dana" Expedition the culturing of oceanic phytoplankton in glass bottles was similarly found to be impossible – unpublished observations by the senior author.

During the cruise of the "Galathea", four series of experiments were made with addition of various nutrients to surface water from the ocean. In order to avoid damage of the plankton algae due to a prolonged stay in the bottles, experimental times from 4 to 5 hours only were employed. It was impossible to discern any effect in any of the four series. The experiments were made in the illuminated tank. Two of these series are presented below. The experiments given in Table 15 were made with ocean water poor in plankton collected about 600 miles northeast of Hawaii. The experiments given in Table

Table 15. Experiments in the illuminated tank with addition of nutrients to surface water enclosed in bottles. 31. March 1952. Position 148°32′W, 26°52′N. Experimental time 5 hours.

	Addition in mg. per litre		Relative rate of photosynthesis
	phosphate -P	nitrate-N	
A	0	0	100
B	0.1	0	97
C	0	0.1	107
D	0.1	0.1	90

16 were made with rather plankton-rich water collected 140 miles South of Panama.

In both series the variation in the rate of photosynthesis is of the same order of magnitude as in the parallel samples – cf. p. 62. Hence no influence of the addition of nutrients could be observed. This, is however, by no means an indication that the nutrients already were present in optimum concentrations in the surface water used for the experiments. This was perhaps the case in the series given in Table 16 but not so in the other series (Table 15). It seems impossible to increase the photosynthetic rate by addition of nitrate and phosphate either momentarily or in the course of a few hours, even if nitrate or phosphate is the absolutely limiting factor – cf. STEEMANN NIELSEN and AL KHOLY 1956. Experimental times of much longer duration would be necessary. As already stated, oceanic plankton does not seem to tolerate such a treatment.

Table 16. Experiments in the illuminated tank with addition of nutrients to surface water enclosed in bottles, 10. May 1952. Position 79°30′W, 6°52′N. Experimental time 5 hours.

	Addition in mg. per litre		Relative rate of photosynthesis
	phosphate -P	nitrate-N	
A	0	0	100
B	0.1	0	103
C	0	0.1	89
D	0.1	0.1	105
E	0.3 ml. distilled water added per bottle (300 ml.)[1]		101

[1] The same amount of distilled water was added to each bottle together with nitrate and phosphate in B, C, D. This special experiment was made in order to prove that the distilled water was not poisonous.

C. INFLUENCE OF LIGHT

The light dependence of photosynthesis in cultures of plankton algae has been rather intensively studied during recent years – cf. RABINOWITCH 1949. The growing of algae in large scale cultures or even in pilot plants has also furthered our present knowledge – see BURLEW 1953. However, plankton growing under natural conditions in the sea shows light dependant features of photosynthesis which cannot be satisfactorily investigated in the laboratory. In spite of all the work already done, our knowledge of the influence of light on phytoplankton production in nature still remains incomplete. During the "Galathea" Expedition an attempt was made to remedy this deficiency to some extent.

At higher latitudes the instability of the water-masses may be an important factor regulating or even impeding the growth of plankton algae – cf. BRAARUD and KLEM 1931, STEEMANN NIELSEN 1935 and SVERDRUP 1953. Under such conditions plankton algae are unable to utilize the light energy penetrating the surface. The duration of the stay of a single cell in the euphotic layer is too short. In none of the areas investigated by the "Galathea" was the instability of the surface water-masses of importance, at least during the time of the year when the expedition visited the area. Discussion of the important question of the influence of instability is hence inappropriate here.

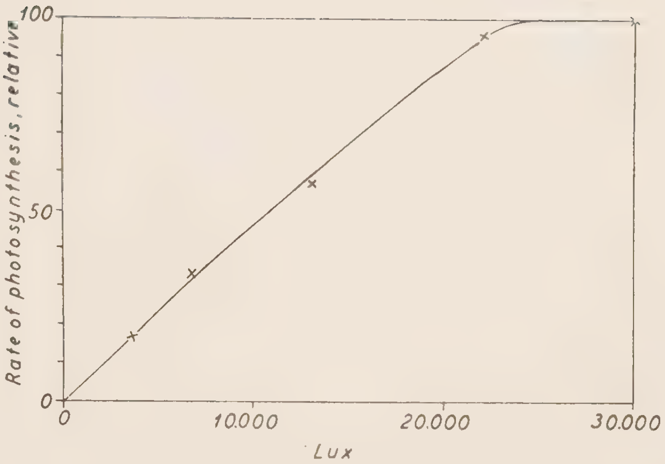
1. Experiments on the dependence on light intensity in marine plankton algae

A knowledge of the dependence on light intensity in the photosynthesis of the marine plankton algae is a necessary background for understanding organic production in the sea. Laboratory experiments using cultures of algae are of only limited importance. The photosynthetic mechanism in algae is highly unstable, and depends on the special conditions during the cultivation. Very few investigations have been made previously on the light dependence in plankton algae just collected in the sea- PETTERSON *et. al.* 1934, STEEMANN NIELSEN 1937. No investigations concerning oceanic plankton have been published previously.

Altogether 12 experimental series with surface water having the normal content of phytoplankton were made during the "Galathea" Expedition. These were made in order to investigate the dependence of the rate of photosynthesis on light intensity. Nine of these series were made with tropical ocean water. As some of the bottles containing the sea water were placed in an open aquarium during the experiments, these could be made only in calm weather. The experimental time was 4 hours for all the twelve series. The experimental procedure is described on p. 61. The temperature was the same as that of the surface water.

Figs. 32-35 show light assimilation curves from

Fig. 32. Light intensity and rate of photosynthesis in oceanic tropical surface plankton (St. 518). Maximum rate = 0.29 mg. C per m.^{3} per hour.



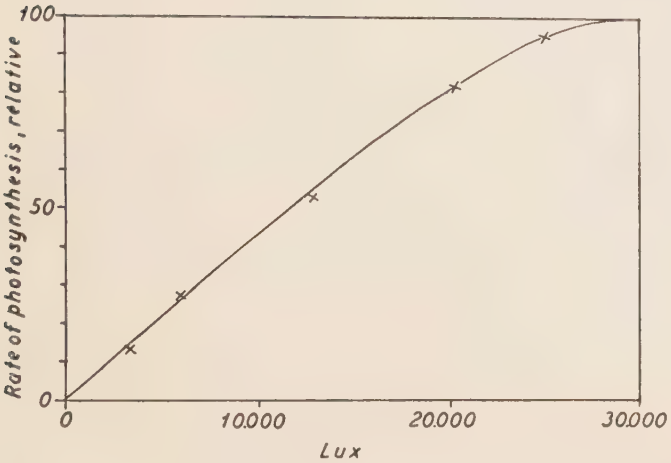
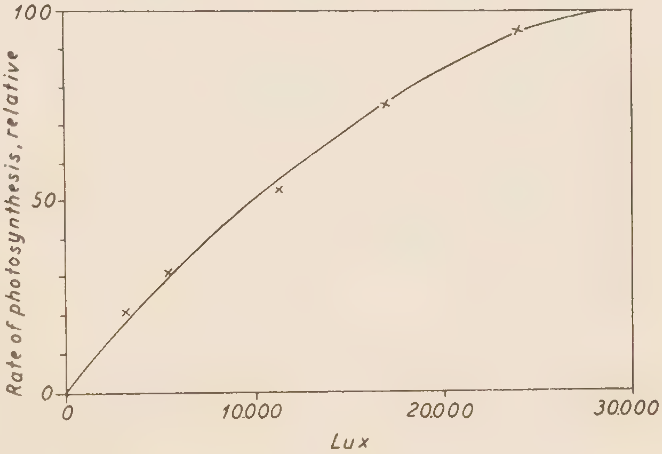


Fig. 33. Light intensity and rate of photosynthesis in oceanic tropical surface plankton (St. 511 a). Maximum rate = 0.52 mg. C per m.^{3} per hour.

Fig. 34. Light intensity and rate of photosynthesis in oceanic tropical surface plankton (St. 515 a). Maximum rate = 0.88 mg. C per m.^{3} per hour.



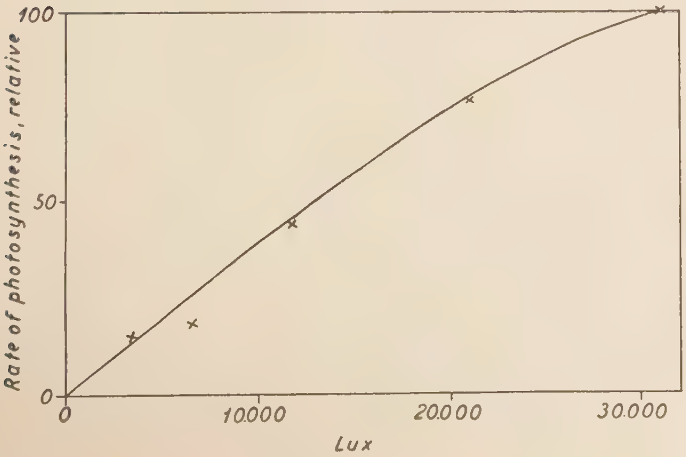


Fig. 35. Light intensity and rate of photosynthesis in oceanic tropical surface plankton (St. 519 a). Maximum rate = 0.41 mg. C per m.^{3} per hour.

four of these experiments with tropical ocean water. The maximum photosynthetic rate was put at 100 per cent. in all experiments. The single measurements are given directly without corrections. The correction factor for C-14 discrimination is without importance for a relative curve, as all single measurements has to be multiplied with the same factor. The rate of dark fixation was not measured in these series. But according to all the measurements of dark fixation in oceanic water the rate varies between about 1 and about 5 per cent. of the rate in optimal light. As the ratio rate of respiration to rate of optimal photosynthesis otherwise would be extremely low, it is better to assume that the rate of dark fixation in the present series was maximum. If the dark fixation is put a 5 per cent, the curves drawn in Figs. 32-35 has to be displaced downward by 5 relative units. To get the curves for net production we have to take into account that about 60 per cent. of the respiratory CO_2 is identical with CO_2 just assimilated (cf. p. 56.). If the ordinate and the curve corrected for 5 % dark fixation would intersect at a point – 5 below zero – as it approximately would do in the experiments presented in Figs. 32-35, the curve for net production and the ordinate would intersect at a point $-\frac{5 \cdot 100}{60} = -8$. The whole curve has to be displaced downwards by another 3 units. The rate of respiration is thus about 8 per cent. of the rate of optimal photosynthesis. If the curve corrected for dark fixation instead has to be corrected to gross production it has to be displaced 5 units upward. This curve is thus identical with the curve drawn according to the original measurements. The curves presented in Figs. 32-35 thus illustrate gross production.

The experiment made at Station 518 (Fig. 32) illustrates the most oligotrophic water investigated by the "Galathea". According to the experiments, the rate of photosynthesis under natural conditions at the surface was 1.5 mg. C per m^3 per day. The curves from all the four experimental series presented in Figs. 32-35 are very similar. They can therefore be treated together. There is found no indication that the curves from very oligotrophic water should deviate materially from those from more normal water – cf. RYTHER 1954.

The slope of the lower linear part of the relative curves was practically the same in all the series where tropical ocean water was employed; 50 per cent. of the maximum rate of photosynthesis was found at light intensities varying between 10.000 and 13.000 lux. The maximum rate of photosynthesis was reached at about 25.000-30.000 lux. It was impossible with the equipment available to make experiments on board the "Galathea" at higher light intensities than 30.000 lux. The "in situ" experiments – cf. p. 58 ff, Figs. 9-12 – give information about the photosynthetic rate at really high light intensities. According to these experiments, the average rate of photosynthesis at the surface during a day is only about 60 per cent. of the average rate at the "best" depth – i. e. the depth showing the highest rate of photosynthesis. The photosynthetic rate at the "best" depth during the day is 70-80 per cent of the maximum rate on the average. It may thus be said that the average photosynthetic rate at the surface in bright weather during the whole day is about 50 per cent. of the maximum rate. During the middle of the day, the rate must be decidedly lower than 50 per cent. The light intensity may be estimated to be about 100.000 lux during the middle of the day. A considerable light inhibition was thus found at this light intensity.

The shapes of the curves (Figs. 32-35) indicate that light inhibition already is of importance at about 30.000 lux. The curves could not be adequately described by the equation of SMITH, 1937, 1938:

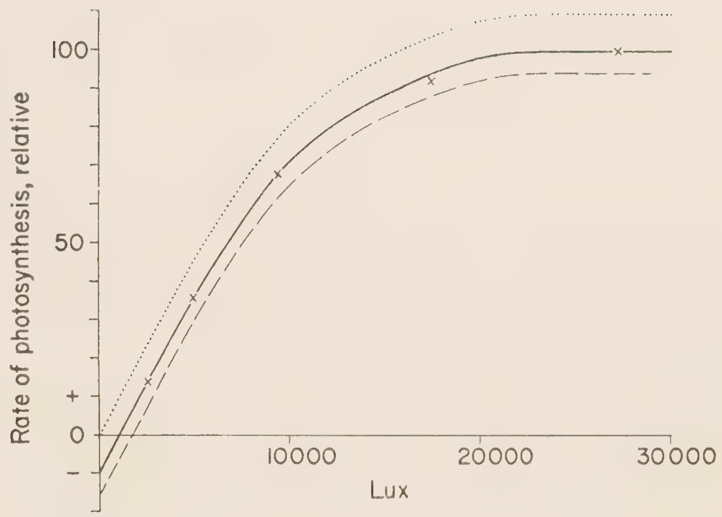
$$K\ I = p/(p^2\text{max}-p^2)^{1/2}$$

in which K is a constant that locates the curve on the I axis, I is the light intensity, p is the rate of photosynthesis at I, and p_{max} is the asymptotic maximum rate of photosynthesis. The equation holds at the lower light intensities but not at the higher. While the theoretical curve continues to ascend, the actual values fall off, indicating the onset of processes other than photosynthesis.

Light inhibition is found near the surface on bright days not only in the Tropics but also in temperate waters during summer – see e. g., STEEMANN NIELSEN 1951. Even in the high Arctic – 70°N – such a light inhibition may occasionally be observed at the surface – unpublished results by the senior author. Working with freshly collected late-autumn plankton from the Sound, Denmark, STEEMANN NIELSEN 1937, in one of the three series under laboratory conditions found a distinct reduction of the photosynthetic rate at the relatively low intensity 23.000 lux, the highest light intensity employed.

The light inhibition directly observed at high light intensities cannot be due to chlorophyll inactivation – cf. STEEMANN NIELSEN 1952 a. The maximum rate

Fig. 36. Light intensity and rate of photosynthesis in the Tasman Sea (St. 599a). Maximum rate = 0.74 mg. C per m.^{3} per hour. Dashed line = net production, dotted line = gross-production.



of photosynthesis is independent of chlorophyll concentration. A chlorophyll-activated decomposition or inactivation of some enzymes of importance in photosynthesis very likely takes place. If the algae showing light inhibition is transferred to a lower, but still saturated light intensity, the rate of photosynthesis gradually regenerates, which shows that the enzymes in question must be re-activated or reproduced; cf. Steemann Nielsen 1949, Fig. 13.

In Fig. 36, a relative light-assimilation curve is presented from an experimental series with surface plankton from the Tasman Sea – 46°S – during the middle of the southern summer. The measurements corrected for dark fixation (1 %) are given directly. If 60 per cent. of the CO_2 given off during respiration is identical with CO_2 just assimilated, the dashed curve represents net production (relative) and the dotted curve gross production (relative).

The rate of respiration is 14 per cent. of the optimal rate of photosynthesis. The compensation point is found at 1.700 lux. The curve for gross production resembles those made with tropical plankton. There is a distinct difference to be seen, however. Half of the optimal rate was achieved at 6.000 lux (10.000-13.000 lux in tropical plankton). In arctic surface water during summer, it is found at about 5.000 lux; cf. Steemann Nielsen and Hansen under preparation.

In contrast to the "Galathea" Expedition, incandescent light, however, was used. Lux is a measure of light without much sense if the sensibility of the human eye is not taken into consideration. A comparison of results after use of light sources with different spectral composition is in fact meaningless.

It was intended to make experiments during the expedition with plankton from the lower depths of the photosynthetic zone. Owing to other work these experiments were indefinitely postponed. During recent investigations in the North Atlantic and in Arctic waters a considerable number of light assimilation curves has been obtained using water collected at all depths of the photosynthetic layer (Steemann Nielsen and Hansen). Fig. 37 presents such a typical curve from the lower part of the photic layer in the Atlantic water south of Iceland. As the dark fixation of C-14 was measured it was possible to construct approximate curves for both net and gross production – the dashed line presents net production. The compensation point was found at about 700 lux. Half of the optimal rate of photosynthesis was achieved at 4.000 lux. The rate of respiration was about 10 per cent. of the rate of optimal photosynthesis. Most of the light assimilation curves of water collected in the lower part of the photic layer have shown a slightly lower ratio of

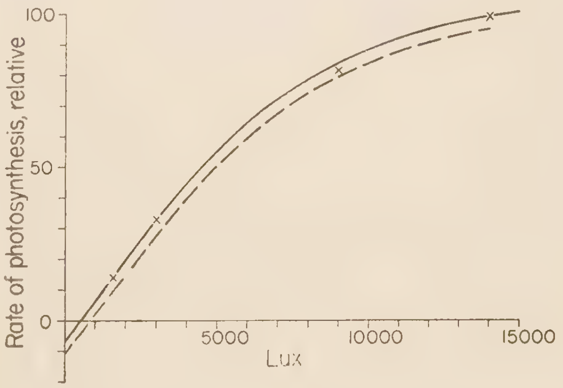


Fig. 37. Light intensity and rate of photosynthesis in plankton from the North Atlantic south of Iceland (latitude 62°N) in the begining of july. Plankton from a depth near the compensation point. Dashed line = netproduction (after Steemann Nielsen and Hansen, under preparation).

respiration to photosynthesis. At most stations the ratio for subsurface water was somewhat lower than the ratio for surface water. This is also theoretically to be expected.

It seems reasonable to conclude that maximum rate of photosynthesis in plankton from the lower depths of the photosynthetic zones in tropical and subtropical waters is achieved at a slightly lower light intensity than in the surface plankton investigated (Figs. 32-36). At 18.000 lux (the light intensity normally used in tank experiments), the maximum rate of photosynthesis was therefore probably often more or less achieved in the plankton originating from the depth where 10 and 1 per cent. of the surface light (blue + green) was measured.

When using the measurements at 18.000 lux with sub-surface plankton to estimate the productivity per surface area according to the formula presented on p. 61, it must be remembered that the formula is derived from experiments with surface plankton. In Nature, the sub-surface plankton receives only the lower light intensities, where the light dependence must be supposed to be more or less concordant both in surface and in sub-surface plankton. It is unimportant that the rate of photosynthesis of sub-surface plankton, contrary to that of surface plankton, possibly does not increase at light intensities above 18.000 lux. Under natural conditions, sub-surface plankton never receives light of such high intensities. As an approximation, the method of calculating the productivity per surface unit may be considered adequate. It must further be taken into account that about three quarters of the total photosynthesis as measured per surface area takes place above the depths where 10 per cent. of the surface light (blue + green) is found. Only about one quarter takes place below this depth – cf. Figs. 9-12.

The light assimilation curves given in Figs. 32-36 are only relative, but the maximum rate per volume of water is also given (gross production). It is of considerable interest to recalculate the curves in terms of photosynthetic rates both per amount of organic matter and per chlorophyll content in the algae.

It seems possible to make the latter recalculation although no special chlorophyll measurements were made during the "Galathea" Expedition. It may be concluded that the initial slope of a light assimilation curve is solely determined by the light absorbed by the active chlorophyll. As the rate of photosynthesis at low light intensities is determined by the rate of the photochemical processes, factors like temperature are without importance. As an approximation only chlorophyll is considered capable of transforming light energy. In thin layers of dilute suspensions of algae it may be concluded that the light absorbed by the chlorophyll is proportional to the content of chlorophyll. Even in leaves of higher plants where the absorption of light is rather complicated due to reflection within the leaf with its numerous airfilled intercellular spaces, GABRIELSEN 1948, Fig. 15, was able to show such a proportinality between light absorption and chlorophyll concentration at low chlorophyll concentrations in the leaves.

Some few light assimilation curves for plankton algae are available, where the chlorophyll concentration is known. We may as an standard use an assimilation curve of *Chlorella pyrenoidosa* grown at 6.000 lux, presented by WINOKUR 1948. In such a culture no chlorophyll is found outside the cells and all chlorophyll inside the cells is most likely in an active state. *Chlorella pyrenoidosa* as grown by Winokur contains 12 μg chlorophyll per mm^3 cells (KOK in BURLEW 1953, p. 65), a statement in accordance with experiences from other laboratories. If a CO_2/O_2 exchange factor of 0.75 is used, 0.36 mg. C is assimilated per mg. chlorophyll per hour at an illumination of 1000 lux.

For comparison we may use an assimilation curve with surface water from the extremely eutrophic Wessling See in Germany presented by GESSNER 1944, p. 725. The stabilization of the water layers in this windprotected lake is so effective that "dead" chlorophyll (i.e. chlorophyll outside living cells) hardly constitutes any important part of the total chlorophyll. If a CO_2/O_2 exchange factor of 0.75 is used, 0.41 mg. C is assimilated per mg. chlorophyll per hour at 1000 lux. This is in accordance with the value obtained by using Winokurs measurements.

Using the standard 0.36 mg. C/mg. chlorophyll per hour at 1000 lux, it is possible to determine the concentration of active chlorophyll in the water used for the experiments presented in Figs. 32-36. They are presented below. Unfortunately these values can hardly be correct. Whereas Winokur and Gessner used incandescent light, fluorescent light was used on the "Galathea". The values of lux thus are not strictly comparable – cf. p. 103. The values presented below should very likely be increased by at least 50 per cent.

Station No.	Fig.	mg. active chlorophyll/m.^{3} surface water
511a	33	0.07
515a	34	0.15
518	32	0.04
519a	35	0.05
599	36	0.16

In comparing chlorophyll directly measured with an ordinary technique and chlorophyll computed from the initial slope of a light assimilation curve, it should be remembered that only active chlorophyll in living algae is included in the latter technique, whereas all chlorophyll is included in the direct measurements. As the plankton used in the present experiments was collected from the surface during the middle of the day some of the chlorophyll may have been inactive. The experiments were of short duration; cf. Steemann Nielsen 1949 and 1952a. The initial slopes of the curves presented in Figs. 32-36 would possibly have been a little steeper, if the experiments had been performed during night, thus showing a higher concentration of active chlorophyll.

It is only possible, approximately – and with reservations – to recalculate the curves (Figs. 32-36) in terms of photosynthetic rate per amount of organic matter in the algae. If using the values for the photosynthetic rate per chlorophyll content, it is necessary to know the relation between the amount of chlorophyll and the amount of organic matter in the algae. No measurements of this kind were made during the expedition. It is a well-known fact that the chlorophyll concentration is low in tropical surface plankton. An analysis during summer of plankton from Dry Tortugas – about 25°N. – yielded a carbon pigment ratio of 0.045, while this ratio averaged about 0.017 at Georges Bank – 42°N., Riley, Stommel and Bumpus 1949. The pigment was unfortunately given in Harvey units, the conversion of which into chlorophyll seems to be variable (cf. Atkins and Parke 1951). As an approximation Harvey's original ratio 1000 H.U. = 0.3 mg. chlorophyll has been used. Using this ratio and assuming the weight of algae to be half that of the total plankton we obtain for Dry Tortugas 5 μg chlorophyll per mg. organic matter in the algae and for Georges Bank 14 μg, values which seem to be in accordance with other experiences.

It is assumed that the plankton from the tropical Pacific water (the light-assimilation curve of which is presented in Fig. 32) has an organic matter: chlorophyll ratio equal to the Dry Tortugas plankton. If the curve is converted to the basis of mg. organic matter produced per hour per mg. organic matter in the algae, the lower curve in Fig. 38 is obtained. The upper curve represents the experimental series from the Tasman Sea (Fig. 36) converted in the same way. The organic matter: chlorophyll ratio is assumed to be the same as at Georges Bank.

As stressed before, the curves presented in Fig. 38 should only be accepted as a first approximation. They are, however, hardly too far from the truth. They would otherwise hardly agree so well with results obtained by determining the organic matter in the plankton by measuring cell volumes – cf. p. 115.

According to the experiment with oligotrophic, tropical waters presented in Fig. 38 (lower curve), the rate of photosynthesis (real assimilatation) is 0.0735 × 12 = 0.88 mg. organic matter per mg. organic matter in the algae per day at 18.000 lux, corresponding to the conditions at the "best depth" – cf. p. 60. If the net production per 24 hours at the best

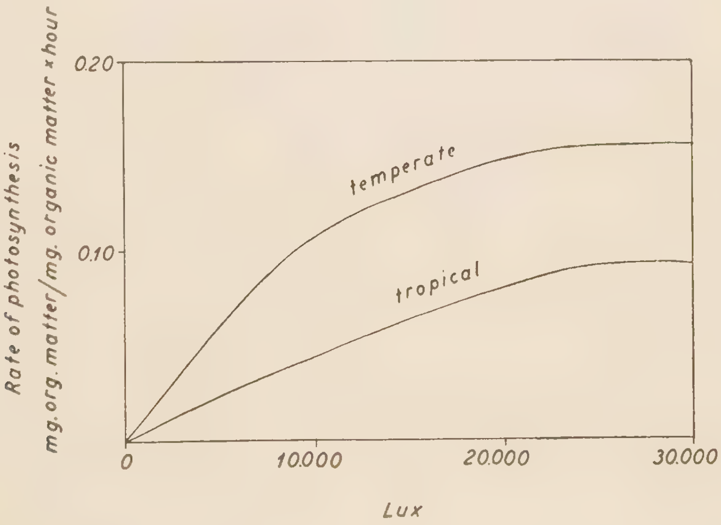


Fig. 38. Light intensity and rate of photosynthesis (mg. organic matter per mg. organic matter in the algae per hour). Upper curve: Tasman Sea St. 599a, lower curve: oceanic tropical oligotrophic surface plankton (St. 518).

depth is put at 0.80 of the gross production we obtain a daily increase here of $\frac{88 \times 80}{100}$ about 70 per cent., assuming no losses due to grazing and sinking. For the whole photosynthetic layer the corresponding increase would be $\frac{88}{2} - \frac{88 \times 20}{100} =$ about 25 per cent. If the population of algae has to remain constant, one quarter of the population in the photosynthesis zone has to be lost every day by grazing and sinking.

According to the Tasman Sea experiments (Fig. 38, upper curve), the rate of photosynthesis (real assimilation) is $0.14 \times 15 = 2.10$ mg. organic matter per mg. organic matter in the algae per day at the "best depth". If the net production per 24 hours is put at 0.80 of the gross production we obtain a daily increase here of 168 per cent., assuming no grazing or sinking, For the whole photosynthetic layer, the corresponding increase would be about 60 per cent. on the average. An increase of this size seems to be rather likely for a productive temperate ocean area during the summer. It seems also to be probable that the increase in oligotrophic tropical parts of the oceans is less than half this size. The values are only approximate of course; but they must, at least be supposed to be of the right order of magnitude. It is nevertheless to be hoped that future investigations may produce more exact values.

2. The utilization of the light penetrating the sea surface by the algae

Compared to the light energy penetrating the surface of the sea only a small amount is utilized by the algae. According to KIMBAL 1928 the average daily light energy at a sea level during a year may be put at about 300 gram calories per cm.^{2} in the tropics and subtropics. Half of the energy is in the visible part of the spectrum. This part is practically identical with that used in photosynthesis. The average daily production of organic matter here may be put at 1.5×10^{-5} g. carbon in the organic matter per cm.^{2} – cf. p. 89, corresponding to 0.06 gram calories per cm.^{2}. This is a utilization of only 0.02 per cent of the total energy and about 0.04 per cent. of the energy in the visible part of the spectrum.

When growing under light of very low intensity, both algae and terrestrial higher plants may utilize as much as 20 per cent. of the incident energy in the visible part of the spectrum under optimal conditions. When they are growing in full sunlight, the maximum conversion is reduced to 2-3 per cent. of the visible part of the spectrum – BURLEW 1953, Chapt. 1 and 5. In the sea a conversion of nearly the same size may occasionally be found – Walvis Bay, cf. p. 75.

The reason why the marine plankton algae normally utilize only a small fraction of the light energy falling on the surface of the sea is, according to all evidence, not due to a poor utilization of the light energy absorbed by the pigments in the algae. In spite of the low chlorophyll content in plankton from the tropical parts of the oceans, the production rate of organic matter per unit of organic matter in the algae is high at optimum light intensity. According to Fig. 38 (lower curve) dealing with algae from an oligotrophic tropical habitat, the maximum rate is 0.09 mg./hour per mg. in the algae. According to the measurements by WINOKUR 1948, the corresponding value in *Chlorella pyrenoidosa* grown at 6.000 lux is 0.17 mg. The Tasman Sea plankton – Fig. 38 upper curve – yielded a value of 0.16 mg. Due to the low chlorophyll content, tropical surface plankton on the other hand utilize the light of low intensities rather poorly.

The reason why only a minimal percentage of the incident light normally is utilized by the algae in the oceans is to be found predominantly in the fact that only a minimal percentage of the light is absorbed by the pigments of the plankton algae. The rest is absorbed mainly by the water but also to some degree by particulate death material and by coloured dissolved organic matter – e.g. "Yellow Substance".

A high utilization of the incident light is possible only if the plankton algae are concentrated in a shallow photosynthetic layer. The light absorption by the water is thus minimised. In the basins of the pilot plants used for growing algae, a daily yield of up till 6 g. C per m.^{2} surface has been obtained, BURLEW 1951. The depths of the water is only a few cm. in these basins. The depth of the photosynthetic layer was only 0.8 m. in Walvis Bay where, as mentioned above, the highest rate of photosynthesis was measured during the "Galathea" Expedition – 3.8 g. C per m.^{2} per day.

The investigations of organic productivity during the expedition shows clearly that the rate per m.^{2} is inversely proportional to the depth of the photosynthetic layer. The data for 184 "Galathea"stations are presented in Table 17. These reveal a marked negative correlation between the vertical extent of the photosynthetic layer and the rate of organic production. For a depth of 100-120 m. none of the stations has a rate of production exceeding 0.24 g. C.

Table 17. Correlation between the vertical extent of the photosynthetic layer and the rate of gross production.

Rate of gross production in g.C/m.²/day	The vertical extent of the photosynthetic layer in metres				
	0–24	25–49	50–74	75–99	100–120
>1	7	3			
0.50–0.99	6	13	12		
0.25–0.49	6	15	17	9	
0.12–0.24	2	6	15	37	12
0.0– 0.11	2	1		9	12

(The numbers within the table are numbers of stations.)

For a depth of 75-99 m. none has a rate above 0.49, the bulk showing a rate between 0.11 and 0.24 g. C. For a depth of 50.-74 m. none of the stations has a rate of production above 0.99 g. C but about a quarter of the stations in this category show rates between 0.50 and 0.99 g. C. For a depth of 24-49 m. a few stations have a rate of production above 1 g. C., but for the most part they are characterized by rates between 0.25 and 0.99 g. C. The stations with the shallowest photosynthetic layer – less than 24 m. – belong essentially to the category with a rate of production above 1 g. C.

All "Galathea" stations were divided into classes according to the depths of the photosynthetic layer: (1) depth 0-10 m.; (2) depth 11-20 m.; (3) depth 21-30 m.; etc. From every class the station showing the highest rate of production was selected. In Fig. 39 these stations are presented; the ordinate gives the rate of production and the abscissa the depth of the photosynthetic layer. The curve drawn thus shows the maximum rate of production found at every thickness of the photosynthetic layer. This curve illustrates even better than the correlation diagram, Table 17, that the rate of production per m.² of the surface is inversely proportional to the thickness of the photosynthetic layer. If the depth of the photosynthetic layer is more than 50 m. a rate of production higher than about 1 g. C/m.² cannot be expected. If the depth of the layer is more than 100 m., a rate of production higher than 0.25 g. cannot be expected.

If the rate of production per m.² is definitely lower than the curve values, the intransparency of the water must be due primarily to causes other than living plankton-algae. Here must be mentioned *inter alia* clay brought out by rivers. The stations in the Atlantic in the neighbourhood of the Congo Estuary – as far as 300 miles away, Table 4, p. 73 – provide typical examples of this kind. Remnants from a considerable production which has been found previously in the water – "yellow matter", detritus – are able to decrease the transparency of the water in the same way. Such an influence may be found at the same place where the high productivity has taken place – such as found after a spring maximum at higher latitudes – or the influence may be found at another place due to transport of the water. A typical example of the latter was found in the area of the Atlantic immediately north of the Benguela Current proper, cf. p. 73.

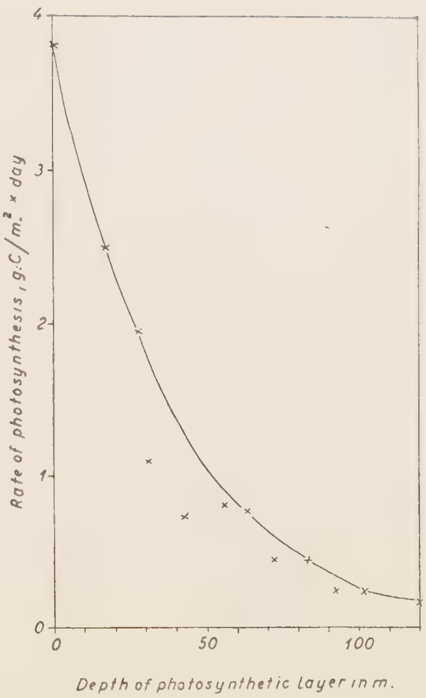


Fig. 39. Depth of photosynthetic layer and maximum rate of photosynthesis per m.² surface.

The water colour is dependent on the transparency of the water. Therefore, the distribution of the water colour in the open ocean outside the influence of land must be closely similar to the quantitative distribution of plankton algae. The charts presented in Fig. 20, p. 78, show this to be true.

Steemann Nielsen 1954 p. 320 ff., has shown that due to the light absorption by the water a high rate of organic production must be considered impossible with a depth of the photosynthetic layer such as occurs in the clearest ocean waters.[1] As the whole matter is obvious, it seems to be pointless to repeat the calculations here. It was shown that in the clearest oceanic water a rate of production higher than about 0.4 g. C/m.^{2}/day must be considered theoretically impossible, and that such a high rate would require in addition absolutely optimum conditions for the algae. This is far from being fulfilled here.

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[1] In a hypothetic ocean free of any particles and dissolved organic matter 1 per cent of green light (525 mμ) and blue light (475 mμ) is found at depths of 90-95 and 160-165 meters respectively. Personal communication by dr. Jerlov. The depth of the photic layer would be about 140 meters.

If the depth of the photic layer is considerable, red light must be considered without importance for photosynthesis or even injurious. Red light under such conditions is only found in water layers where the light intensity is supra-optimal – cf. Figs. 9-12. Red light includes about $^1/_3$ of the photosynthetically active light.

3. The influence of weather conditions and of seasons on the rate of organic productivity

The light reaching the surface of the sea varies according to both the season and the weather conditions. In the present work, only the conditions in the Tropics and Subtropics will be discussed. Considerable information concerning organic productivity in temperate and arctic seas has now been collected from Danish sources. This material is to be presented in a special publication.

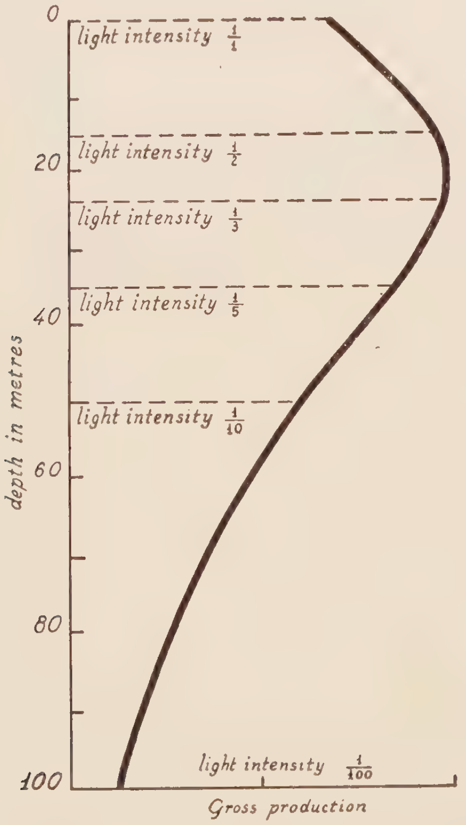

Fig. 40. Light intensity and rate of gross production at the different depths – cf. the text.

It is in fact a matter of convention to speak about limiting factors for organic production. In one way light may always be considered a limiting factor, since a reduction of the light reaching the surface will reduce the organic productivity per area in all cases momentarily as will be shown below. The whole matter is much more complicated however. All factors affecting organic productivity must be regarded as complex. A series of factors may apparently all appear as limiting and they are really so under the normal steady state conditions found in Nature.

If, however, one of these factors – e.g., light – would be permanently changed, the whole mosaic of factors would create a new equilibrium. It is thus quite likely that a permanent reduction of the light intensity at the surface (to e. g. 50 per cent. of its normal value without the other factors being affected – a rather improbable condition in Nature) in the long run would have very little influence on the organic productivity as measured per surface area. The considerations given below thus concern only the instantaneous effects which influence organic productivity by reducing the light reaching the surface.

Let us consider a tropical station at which the depth of the photosynthetic layer is 100 m. If the plankton algae are evenly distributed in the layer – and the light absorption is the same at all depths – we obtain the hypothetical curve shown in Fig. 40. This represents the daily relative rates of total photosynthesis at the different depths on a clear day. The maximum rate is found at depth of about 20 m., where the average of the blue and green parts of the light falling on the surface is reduced to nearly one-third. As the rays of the red part of the spectrum are completely absorbed in the upper 5 to 10 m., for the sake of clearness although not correctly we may disregard this part of the light. The light intensity being too high near the surface causes a reduction in the rate of photosynthesis.

If the light falling on the water surface is reduced through-out the day to one-third, the rate of photosynthesis at the surface is the same as that taking place at a depth of 24 m. on a clear day. With a decrease of the light intensity to one-third, the photosynthetic rate per unit volume of surface water (g. C/m.^{3}) thus increases by nearly 50 %. However, the photosynthetic layer is now only 76 m. deep. The curve for a light intensity of one-third is identical with that (Fig. 40 light intensity $\frac{1}{3}$ at the surface) which would be obtained if the curve is shifted bodily 24 m. upwards. The rate of total photosynthesis measured per square metre (g. C/m.^{2}/day) is thus about two-thirds of that measured at the light intensity $\frac{1}{1}$ at the surface. By reducing the light intensity at the surface to one-tenth, the curve (Fig. 40) has to be moved bodily 50 m. upwards, which reduces the depth of the photosynthetic layer to 50 m. The rate of total photosynthesis at the surface as g. C per cubic metre per day decreases about 15 % (or less-because of the red light) and the rate as g. C per square metre per day decreases to about 25 % of the rate at light intensity $\frac{1}{1}$ at the surface.

A day with a light intensity of only one-tenth of that on a normally clear day is in fact a very dark one, for example on which rain falls throughout the day. Only in such very dark weather does a slight reduction of the photosynthetic rate occur (per unit volume) at the surface.

The rate of photosynthesis below a unit area is affected somewhat more by the weather conditions, but the rate is seldom reduced by more than 50 %. On extremely dark days only, the rate is reduced by about 75 %.

If other hydrographic conditions are the same throughout the year, no important variations in organic productivity are presumably to be expected in the tropical parts of the oceans. In the subtropical parts the variations between summer and winter are believed to be fairly small. According to Table 25 in SVERDRUP *et. al.* (1942), in the Sargasso Sea at 30°N the average amount of radiation from sun and sky which reaches the sea surface in the darkest month of the year (December) is about 50 % of the amount in the brightest month (August). According to Fig. 40 with the other factors assumed to be the same, the rate of organic production per unit area in the darkest month is about 80 % of the rate in the brightest month. In this calculation no consideration is taken of the fact that a seasonal change being a long term change will try to create a new permanent equilibrium, thus reducing the influence of the variation of a single factor – cf. above.

D. INFLUENCE OF TEMPERATURE

Variations in temperature strongly influence the rate of respiration and the rate of photosynthesis at a high light intensity. This is true both for plankton algae and for all other autotrophic plants. It does not necessarily mean that the rate – measured per dry weight – is lower in the Arctic than in the Tropics. On the contrary, the two curves from a tropical and a temperate ocean area, presented in Fig. 38, p. 105, seem to indicate just the opposite, a result of the higher concentration of chlorophyll in the algae from the latter environment. A higher concentration of the enzymes participating in respiration and photosynthesis may counteract the depressant effect of the low temperature in the Arctic. Marine phytoplankton has not been studied in this respect. Several authors – e. g., SPÄRCK 1936 – give examples of cases in which the rate of respiration of a specific animal species is less at the same temperature for individuals which have been collected from a warmer environment than for individuals collected from colder waters. If this occurs with individuals of the same species it is probably even more pronounced when cold- and warm-water species are compared. There is no reason to believe that in this respect plants are different.

The extent to which organic productivity in the sea is directly influenced by temperature is not known.[1] The indirect influence of this factor is most likely the more important. Low temperature often seems to have a pronounced effect through inhibiting the activity of bacteria. An increase in temperature may perhaps particularly accelerate the regeneration of the nutrient salts, with the result that organic production is also accelerated.

The reason why areas in the Tropics with shallow depths practically all show a rather high rate of organic production must be ascribed primarily to the high temperature at the top of the bottom-sediments; thus a high regeneration rate of the nutrient salts is caused. By diffusion and other mechanisms the nutrient salts are transferred into the water layers above and have an almost immediate effect on the organic production of the phytoplankton. The bacteriological decomposition in the surface water of the open oceans seems to be rather limited in scope. The supply of nutrient salts seems to be effected mainly in other ways. A high temperature of the surface layers must be supposed to be of only little importance for the organic production here. The production rates measured in the open sea seem to confirm this supposition.

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[1] Recent investigations in the North Atlantic and in the Arctic seem to indicate that the direct influence of temperature on the rate of organic production is rather limited.

E. INFLUENCE OF SINKING AND GRAZING BY ANIMALS

The importance of grazing for the production of plankton algae was already mentioned by early investigators, thus by Lohmann 1908 in his outstanding treatise on the plankton near Kiel. Later, Harvey *et. al.* 1935 have contributed to the problem. Fleming 1939 published some important theoretical considerations. Cushing 1955 has given an interesting contribution concerning the conditions in plankton patches found in the North Sea.

As shown so convincingly by Hentschel 1932-1936, the concentration of phytoplankton is extremely constant in the different areas of the Atlantic in tropical and subtropical latitudes. The phytoplankton is, however, constantly growing. According to the experiments concerning the light dependence of production presented on p. 101, the growth rate must be rather substantial even in the oligotrophic parts of the oceans.

If the lower curve given in Fig. 38 is taken as the standard for the oligotrophic tropical parts of the ocean, 0.89 mg. organic matter is produced per 12 hours at 18.000 lux per mg. organic matter in the algae. This is the gross production. 12 hours at 18.000 lux correspond to 12 hours at the "best" depth" – cf. p. 60. The daily average for the whole photosynthetic zone is thus $0.5 \times 0.89 = 0.45$ mg. per mg. of the algae. If the respiratory rate for 24 hours is put at 40 per cent of photosynthesis, the average daily net production per mg. algae organic matter is 0.25 mg. If no loss of algae took place, the algal concentration would be doubled in about 4 days. As this does not happen, there must be a simultaneous loss of algae amounting to about $^1/_4$ of the algae daily, on the average.

This loss may be due to 1) sinking below the photosynthetic layer, 2) grazing by animals and 3) death and decay of the algae. The last possibility will not be discussed here as it must be assumed to be of minor importance only. No real information is available. Cushing 1955 uses the percentage of empty diatoms as a measure. Empty diatoms may, however, result from their consumption and excretion.

Sinking, on the other hand, must be assumed to be of considerable importance. The vertical plankton distribution in the South Atlantic according to the "Meteor" gives very instructive information. Hentschel 1936, Abb. 68, has shown that according to the whole material from the expedition the concentration of total plankton at a depth of 100 m. is less than $^1/_{10}$ of the concentration at the surface. At 200 m. depth it is less than $^1/_{100}$. This figure is a little misleading, however, as the coastal stations with a shallow photosynthetic layer and a high concentration of plankton tend to reduce the relative concentrations at the depth of 100 m., 200 m. and more.

We have therefore taken the 25 stations from the central minimum area of the South Atlantic – profiles VI, VII and VIII – and computed the average plankton concentrations at the different depths 0-1000 m. We have taken only the sum of coccolithophorides, diatoms and dinoflagellates, thus including all the important producers of organic matter. The distribution of plankton is rather homogeneous in this area.

As the depth of the photosynthetic layer is a little more than 100 m. in the area in question, it is seen that the concentration of phytoplankton at a depth of 200 m., i.e. at a depth less than 100 m. deeper than the lower boundary of the photosynthetic layer, is decreased by a factor of 10; cf. Table 18.

In the next 200 m. the phytoplankton concentration drops only by a factor of about 5; per 100 m. thus by a factor of only 2.2; in the next 300 m. by a factor 1.5 per 100 m. and in the next 300 m. by a factor 1.1 per 100 m. If the sinking rate is the same in all these water layers – a supposition which, however, by no means has to be correct – it means that the rate of grazing must be considerably higher in and near the photosynthetic layer than further below. This is, however, not surprising. It must be assumed that there is a lower concentration limit for phytoplankton below which the grazing animals cannot afford to work. Unfortunately the whole matter of grazing is only little investigated (cf. e.g. Gould 1951). We can, however, from the presence

Table 18. The vertical distribution of phytoplankton (coccolithophorides, diatoms, dinoflagellates) in the central minimum area of the South Atlantic (calculated after Hentschel).

Depth in m.	Number of cells per liter
0	2600
50	3600
100	2400
200	287
400	60
700	16
1.000	13

of grazing animals in the oligotrophic parts of the ocean, conclude that it is possible to collect sufficient food by eating plankton algae at least in the photosynthetic layer and a little further down, although considerably more work must be done by the zooplankton compared to the work necessary in more plankton-rich water.

In the photosynthetic layer, the highest plankton concentration is found at a depth of 50 m. Both at the surface and at a depth of 100 m. the concentration is considerably lower. This vertical distribution is in rather good agreement with the vertical distribution of potential productivity as found in areas of the same kind during the "Galathea" Expedition.

An attempt was made to obtain information on grazing by experiments on the "Galathea". Very little faith was put in these experiments however. It is far from certain that the grazing animals behave normally when enclosed in a rotating bottle as was used in these experiments. Further, only 300 ml. water samples could be used, a quantity very far from being representative of an open ocean in respect to the grazing organisms. According to Hentschel, less than 10 metazoes were found per 4 litres in the upper 50 m. layer in the oligotrophic parts of the Atlantic – cf. Fig. 20d. p. 78. The experiments were made at 56 stations altogether, all during the latter part of the expedition.

These were made by taking water from the surface and illuminating three 300 ml. samples in the tank for 4 hours. One sample was filtered through finest bolting silk (No. 25) before the start of the illumination, one was filtered in the same way after the end of the illumination, and one was not filtered at all. The difference between the photosynthetic rate of the first and the second of these samples should theoretically represent a measure of grazing; other explanations may be given, however. The phytoplankton from the open ocean often seems to suffer somewhat by being filtered through the silk. At the majority of the stations a slightly higher photosynthetic rate was found in the samples filtered after the experiments than in the samples filtered before, thus indicating a damage of the photosynthetic capacity by filtering.

At some few stations "grazing" was possibly observed experimentally. However, it seems safest not to put any stress on these observations.

As shown on p. 106 the daily loss of phytoplankton in the photosynthetic layer in the tropical oligotrophic parts of the ocean amounts to about 25 per cent. – equal to the daily increase due to photosynthesis. The lower curve (Fig. 38) was taken as a standard. In temperate parts of the ocean on the other hand, the rates of both processes are pronouncedly higher. If the daily increase in organic matter in the Tasman Sea – see the upper curve Fig. 38 – is treated in the same way as done for the station given in the lower curve the daily increase of organic matter in the whole photosynthetic layer amounts to 60 per cent. The daily loss due to sinking and grazing therefore may be expected also to be about 60 per cent. The daily increase of organic matter is very likely somewhat higher in really eutrophic areas both in the Tropics and at higher latitudes.

Without a mathematical treatment it is difficult to estimate how much of the losses in the photosynthetic layers are due to sinking and how much are due to grazing. If we consider all water layers as a whole, however, most of the plankton which is lost in the photosynthetic layer ultimately seems to be eaten by animals. The vertical distribution of phytoplankton normally found indicates that a considerable rate of grazing must take place in the water layers immediately below the photosynthetic zone. It would otherwise be difficult to understand how the phytoplankton concentration drops by a factor 10 per 100 m. in the first 100 m. below the lower limit of the photosynthetic layer, whereas it only drops by a factor varying from 1.6 to 1.1 per 100 m. between 400 and 1000 m. – cf. Table 18 p. 110. It may be supposed that about 95 % of the algae consumed daily is eaten in the uppermost 200 m.

In the Appendix 2, Mr. K.P. Andersen, M. Sc. has treated the "Meteor" counts presented in Table 18 mathematically. By means of some simple assumptions and the rates published in the present work regarding the production of organic matter in the oligotrophic tropical-subtropical parts of the oceans, the rate of the grazing going on at the different depths and the sinking velocity are computed. The latter (about 11 m per day) is comparable with the velocity for such areas given by other workers, Riley, Stommel and Bumpus 1949. According to Mr. Andersen's calculations 99 per cent. of the algae consumed is eaten in the uppermost 200 m. The sinking velocity is most likely estimated somewhat too high. This is mainly due to a specific oligophotic plankton being found first of all at a depth of 50-100 metres.

The rates of grazing offered by Mr. Andersen in the appendix 2 in terms of number of algae eaten have been converted into mg. carbon per m.^{3} and day. The total grazing has been put at $60 \times 0.75 = 45$ mg. carbon/m^2 $\times$ day (= net production). As mean values for grazing in the central, tropical + subtropical, oligotrophic areas of the oceans we obtain the following mean values.

depth in m.	grazing (mg. carbon/m.^{3} per day)
50 – 0	0.24
100 – 50	0.35
200 – 100	0.14
400 – 200	0.01
> 400	< 0.01

We may thus conclude that the animals eating phytoplankton seem to be able to handle the grazing effectively even in the oligotrophic parts of the ocean. How they manage to deal with the considerable volume of water necessary is another problem not yet adequately solved – cf. CUSHING 1955. It must, however, be supposed to cost a considerable amount of energy to collect the necessary food in oligotrophic water, as already pointed out on p. 110. Whereas the major part of the food digested may be used for growth if food is plentiful, only a minor part may be supposed to be available for growth if food is scarce, the major part being used for the production of energy necessary for collecting food. It could therefore be expected that the mean lifetime for the single individuals of zooplankton animals is much longer in oligotrophic areas than in eutrophic areas. Although the production of these animals is low, the standing crop may be relatively higher. In Section H some indications of this will be presented.

One of the last links in the food cycle – the fishes – according to all evidence are scarce in the extremely oligotrophic parts of the oceans. This is presumably a necessary condition for the existence of a relatively high – although in reality nontheless low – standing crop of zooplankton. It may perhaps be concluded that a certain minimum concentration of zooplankton is necessary for most fish species. Below that concentration fish cannot exist at all; at least only a few especially adapted species. The concentration of zooplankton in the most oligotrophic parts of the oceans is thus probably too low for maintaining a real stock of many fish species, although this zooplankton has a higher concentration – higher standing crop – than expected according to its production. It may be mentioned that oceanic birds, which also are dependent on the zooplankton, are practically absent in the very oligotrophic parts of the oceans like the Sargasso Sea – cf. JESPERSEN 1937.

From certain quarters – cf. HARVEY 1955 – the idea is continually put forward that a harmonic balance is unlikely to occur in nature, where the animals enjoy alternating periods of overeating and starvation and where the equilibrium between standing crop of plants, herbivores and carnivores is continually passing in and out of balance.

Against this assumption it may be mentioned that those investigations which technically may considered by far the most reliable present evidence of just a very significant and constant balance between the phytoplankton and the zooplankton. The investigations in the Baltic near Kiel by LOHMANN 1908 and by HENTSCHEL 1932-1936 in the Atlantic must be mentioned particularly. The present investigations give further evidence from the oceans, just as unpublished recent investigations in Danish Waters and in Danish Lakes. The problem is discussed further in Sections F and H.

F. THE INTERACTION OF THE FACTORS LIMITING OR CONTROLLING THE PRODUCTION OF ORGANIC MATTER IN THE SEA

In the introduction to this section it was stressed that the different factors influencing the organic production hardly can be treated separately. In spite of this, these factors were discussed separately. Due attention was paid to the indirect influence by other factors. An attempt at synthesis will now be made.

Taking all seas as a whole, it may be stated – as an approximation at least – that the replenishment of the nutrients in the productive surface layers is the essential factor determining the size of organic productivity. The amounts of nutrients – particularly nitrate and phosphate – which annually are made available for the plankton algae by upwelling, turbulence and regeneration, determine the total productivity of all oceans. For instance if we knew exactly the annual replenishment of phosphorus in the surface layer of all seas we could compute the total productivity measured as carbon by multiplying the phosphorus content by a factor of 40-50, as was done for certain special areas.

Generally speaking, it may be stated that light as a whole is available in sufficient quantity to provide the energy necessary for a production equivalent to the annually available P and N in the surface layers. In certain areas or at certain times of the year, light energy is insufficient locally or temporarily. In areas with upwelling, the whole amount of nutrient salts conveyed to the surface is mostly not utilized at that place; the nutrients are distributed over a much wider area by horizontal currents. At high latitudes during winter, light is insufficient for a production utilizing all of the nutrient. During the spring maximum however this takes place. Integrated over the whole year and for all seas, light energy is sufficient to keep in step with the replenishment of the nutrient salts. Some parts of the Antarctic must probably be excluded, because of too strong vertical mixing affecting too poor light conditions for the single algae, leading to a decrease in the organic production. The phytoplankton is not able to utilize the light during the summer to the extent that all phosphate and nitrate near the surface is assimilated (GRAN 1931).

As a theoretical possibility it could be supposed that the light intensity reaching all sea surfaces would be increased by e.g. 50 per cent. The total annual organic production would then be supposed to increase in the sea. However, the main reason for this increase would, not be primarily the direct effect of the increase in light intensity on photosynthesis, but mainly the more indirect effect due to an increased water circulation in the oceans together with a faster regeneration of the nutrient salts due to an increased temperature in the seas.

On p. 108 the effect of a temporary variation of the light intensity on the organic production was discussed. It was also shown here that the two factors, light intensity and nutrient supply, mostly are matched in such a way that apparently they both seem to act as limiting factors at the same time. If nutrient supply is high, the depth of the photosynthetic layer is shallow due to absorption of light by the big standing crop of algae. A considerable part of the light is thus used for photosynthesis. If, on the other hand, the nutrient supply is scanty, the depth of the photosynthetic layer is considerable, since the population of algae absorbs only a small proportion of the light and utilizes it for photosynthesis. The major part of the light is thus absorbed by the water. In both cases a temporary decrease of the light intensity due to weather conditions influences the organic production. As the light intensity during a clear day is superoptimal for algal photosynthesis near the surface, the decrease in productivity on dark days is only rather limited (see p. 109).

In section D the idea was stressed that the influence of temperature on organic production primarily is indirect. An increase in temperature increases the bacterial and enzymatic regeneration rate of the nutrient salts. The influence of the last mentioned factor, grazing, seems to be of a much more complicated nature. Grazing certainly is of importance for the regeneration of the nutrient salts, since the first steps in these regenerations consist mostly of processes going on in the grazing animals after the algae have been eaten by them.

The influence of grazing is much more intricate, however. Regeneration of the nutrients can take place without the help of the animals eating the algae, although grazing certainly is of importance in this respect. At least as important, however, is the influence of the grazers in maintaining the stock of plankton algae at a level suitable for the available growth conditions. Whereas the supply of nutrient salts and partly light energy may be characterized as the limiting factors for the organic production, grazing may be better characterized as the controlling factor. Without grazing, organic production by the plankton algae could not be maintained under the static conditions mostly found in Nature. The consumption of algae by zooplankton has the effect that plankton algae in Nature rarely are found in a state where their growth is absolutely limited by deficiency in nutrient salts.

When growing plankton algae in cultures under laboratory conditions, quite another picture than that normally seen in nature is mostly obtained. In the laboratory, lack of nutrients – e.g., those containing N and P – in a very short time produce an absolute deficiency of these elements, – cf. AL KHOLY 1956. The algae are transferred into a state where they are not growing at all. The respiratory rate is more or less unaffected, while the rate of photosynthesis is much reduced. After a renewed supply of the lacking nutrient, it takes a considerable time – in *Chlorella* thus more than 24 hours – before growth is starting again – AL KHOLY 1956. The rate of photosynthesis is unaffected for at least many hours – cf. STEEMANN NIELSEN and AL KHOLY 1956.

If no grazing animals were found, e.g., in the oligotrophic, tropical parts of the oceans, we should very likely expect short periods with relatively much plankton alternating with long periods when practically no algae were found. Hentschel's investigations during the "Meteor" Expeditions have indisputably shown that on the contrary the standing crop of algae is exceedingly constant here both in regard to place and time. If no grazing animals were present, a population of plankton algae would be assumed to absorb completely the nutrient salt being most pronouncedly in the minimum. The algae would continue growth until the element in question would be in absolute minimum also in the cells of the algae. Growth would thereafter stop completely and the population would slowly but steadily sink into deeper water layers. As the replenishment of the nutrient salts is a slow process in the area in question, it would probably take a considerable time before new production of algae could be started.

The presence of the grazing zooplankton alters the picture completely. The development of an algal population able to utilize the nutrients completely and to produce absolutely deficient algae, is prevented. The result is the existence of a small but rather stable population of plankton algae. The growth rate is certainly reduced compared to the rates found when a higher supply of the nutrient salts is available. A daily growth rate of about 25 per cent. per day on the average in the photic zone may be estimated for these oligotrophic areas – cf. p. 106. This growth rate is identical with the daily loss due chiefly to the grazing by the zooplankton. Remarkably stable populations of algae and animals are thus found, as was shown by HENTSCHEL 1933.

According to the important contribution by FISH 1954 concerning the zooplankton in the northern Sargasso Sea, there seems to be a rather marked biological cycle here. Short periods of relatively high – although in fact low – zooplankton concentrations alternate with periods of very low concentrations. It must, however, be kept in mind that because of the rather coarse silk used for the nets, such as also mentioned by Fish, nauplia and the early stages of the small copepods were not caught. Per cubic metre only about 200 metazoa on the average – mostly copepods – were found. In the central part of the South Atlantic Eddy – comparable with the Sargasso Sea – HENTSCHEL 1933 using a technique applicable also for animals of small size, found at least 5 times as many metazoa per m.^{3} on the average. No marked fluctuation – neither seasonally nor locally – in the total number of metazoa was indicated in the South Atlantic Eddy as Hentschel otherwise scarcely would have been able to demonstrate such an even distribution of zooplankton.

It seems thus rather likely that in waters like the Sargasso Sea no great variations in the total amount of "grazers" are found. The fluctation found by Fish seems principally to be explained by sequences of periods with a maximum of adult organisms alternating with periods where the zooplankton mainly consists of juvenile animals not caught by the nets employed. The short period numerical fluctuations in adult animals shown by Fish are nevertheless of principal importance.

The station worked by Fish in the Sargasso Sea was located as high to the north as latitude 35°N, where the annual fluctuation in the temperature of the upper water masses is far from negligible. The conditions for the zooplankton differ thus markedly between summer and winter. However, in the really tropical part of the oceans rather similar fluctuations in the zooplankton probably occur. These fluctuations, as in the Subtropics, would concern principally the composition in species and age groups, not the total number of grazers.

As static conditions seems to be found in most tropical parts of the oceans, the size of the standing crop of zooplankton must be assumed to be directly dependent on the size of the algal production, or better perhaps on the growth rate of the algae under static conditions.

The detailed mechanisms of this very complicated and intricate interrelation between zooplankton production and phytoplankton production are at present beyond our knowledge. We must be content with admiring Nature. It seems rather likely that external metabolites excreted by animals and plants at least have som influence on the growing rates of the plankton algae and the animals, and thus also on the establishment of an equilibrium between the plants and animals – cf. LUCAS 1947, RICE 1954.

In the northern latitudes, growth conditions for the plankton algae may often suddenly shift from being very poor to being exceedingly favourable. In the North Atlantic south of Iceland, a calm period during May thus has the effect that the water masses become stabilized due to the heating of the surface layer – cf. STEEMANN NIELSEN 1935. The low standing crop of algae – a consequence of the lacking stability – increases immediately and very quickly. At first very little grazing takes place. After the establishment of a big standing crop of phytoplankton, the grazing rate increases rapidly preventing an unlimited further growth of the algae. In some way or other, the breeding of the zooplankton in these waters must get started due to the phytoplankton production. According to MARSHALL and ORR 1952, the egg production by the hibernating specimens of the zooplankton is affected by a growing phytoplankton.

Not even Nature always seems to function perfectly. From northern latitudes, e. g., patches of the brown flagellate *Phaeocystis Pouchetia* are known. It seems that quantities of this flagellate under certain conditions exclude the zooplankton. This again seems to have the effect that the flagellates grow without control – cf. HARDY 1936b.

In all probability in some areas with special hydrographic conditions the standing crop of zooplankton occasionally may be temporarily or locally too big in comparison with the growth rate of the phytoplankton. Overgrazing will thus occur, but it seems to be on the whole without much importance in the oceans – see further p. 117.

G. STANDING CROP OF PHYTOPLANKTON AND ORGANIC PRODUCTIVITY

As already pointed out in the Introduction, the agreement in the oceans between the standing crop of algae as measured by plankton counts after centrifugation and the organic productivity by the algae seems to be surprisingly high. The quantitative picture of an ocean on the basis of the counts made during the "Deutschland" and the "Meteor" Expeditions seems to be identical in all respects with the picture to be drawn according to the measurements of organic productivity made during the "Galathea" Expedition. In most freshwater lakes a high correlation is also found between the concentration of chlorophyll and the production – cf. GESSNER 1944.

It is of considerable interest to try to transform the plankton counts into organic matter. For the most oligotrophic parts of the Atlantic Ocean, the volume of all counted algae per m.^{3} surface water according to relative abundance and size of the different species (HENTSCHEL 1932) has been estimated to be about 3.5 mm.^{3}. According to Hentschel about 3000 cells per litre were counted. If, according to WINOKUR 1948, a factor $\frac{1}{10}$ is used for converting volume in mm.^{3} to carbon in mg. about 0.35 mg. carbon bound in the autotrophic algae is thus found per m.^{3} surface water. If the light-assimilation curve from the oligotrophic oceanic surface water is used (the lower curve, Fig. 38), a rate of photosynthesis of about 0.025 mg. carbon per hour per m.^{3} at 18.000 lux should be expected. The surface water at the three "Galathea" stations in the Sargasso Sea (762, 763, 764) gave on the average a photosynthetic rate per hour of 0.069 at this light intensity. The measured production rates are thus nearly 3 times the rates computed according to Hentschel's plankton counts. It must, however, be taken into account that his centrifugation technique caused a rather considerable underestimation of the number of cells present. Comparative studies using at the same time another established method have indicated that in oceanic water about $^2/_3$ of the plankton cells may escape enumeration in the technique used by Hentschel (cf. STEEMANN NIELSEN 1933, SCHMIDT-RIES 1936 and BERNARD 1953). The statement by BALLANTINE 1953 that about 100 per cent. correct plankton counts may be obtained by a similar centrifugation technique concerns only the special conditions used by her. The plankton which was found in relatively high concentrations was concentrated by her only by a factor 10 – as against a factor 1000 used in normal plankton work.

As another example, an area of quite a different kind may be chosen. In the very plankton-rich water off the coast of Africa between 15°S and 25°S, HENTSCHEL 1932 found a plankton concentration of about 300.000 cells per litre. If the cell volume of counted algae is put at 350 mm.^{3} per m.^{3} and the loss of cells due to the technique is put at $^2/_3$, the total volume per m.^{3} is 1000 mm.^{3}, which again is equal to 100 mg. carbon per m.^{3}. By using the Tasman Sea curve – the upper curve, Fig. 38 – the photosynthetic rate at 18.000 lux is 14 mg. carbon/m.^{3}/hour. The photosynthetic rate at 18.000 lux of surface water at the four "Galathea" stations in this area (132, 136, 138, 143) varied between 3.5 and 18 mg. C/m.^{3}/hour (on the average 11 mg. C).

It can thus be stated that the measurements of the standing crop of algae investigated by the "Meteor" Expedition and the measurements of organic productivity during the "Galathea" Expedition are in rather good agreement, both in the most oligotrophic and in the most eutrophic part of the ocean. In the tropical parts of the Atlantic where the life conditions for the phytoplankton must be assumed to be very stable, variations from seasons to season and from year to year most likely are small only. There should be no reason not to compare the plankton from the "Meteor" and the "Galathea" expeditions although nearly 25 years lay between the two expeditions.

It is of course always better to compare the standing crop of plankton algae measured simultaneously with the determination of the organic productivity. At higher latitudes this is a condition *sine qua non*. From Danish waters, a multitude of such simultaneous observations is now available, which will be published elsewhere.

In the Danish investigations the plankton counts are made with Utermöhl's method (inverted microscope) – using formalin-preserved material. Such a procedure is mostly adequate, but not always. If diatoms predominate, the technique is excellent. Sometimes, however, the main bulk of algae consists of fragile flagellates which disintegrate when preserved with formalin.

Therefore, as an example of the correlation between the organic production and the standing crop of algae computed by counting the algae and measuring their cell volumes, some comparative studies made in two Austrian lakes together with Professor F. Ruttner, Lunz, will be quoted instead. The plankton counts and the determinations of cell volumes were made by Professor RUTTNER by means of fresh material. In the table presented above the gross production in mg. C per m.³ per day from the water layer showing the optimum light conditions for photosynthesis is compared with the standing crop of algae expressed as mg. C/m.³. It is supposed – as done elsewhere in this treatise – that 1 mm.³ algae is equivalent to 0.1 mg. C.

	Gross production mg.C/m.³ per day	Standing crop mg.C/m.³	Gross production (mg.C/m.³ per day in percentage of standing crop) mg.C/m.³
Lunzer Untersee 21.7.53	18.5	14.6	127
– – 27.7.53	14.2	10.9	130
Lunzer Obersee 25.7.53	66	47	140

If the chlorophyll concentration at a maximum is put at 4 per cent. of the organic matter in the algae, we may at a maximum expect 1.5 mg. chlorophyll per m.³ in the Untersee at the 21th of July and 1.1 mg. at the 27th of July. According to GESSNER 1944 2 mg. chlorophyll was found per m³ in the Lunzer Untersee in July 1941. The maximum rate of photosynthesis at an optimum light intensity may for the 21th July be estimated at about 7.5 mg. CO_2/m.³ per hour. The assimilation number is thus about 5 at minimum, which is in accordance with the assimilation numbers given for plankton from similar lakes, e.g. by GESSNER 1944. It may be mentioned that the assimilation numbers stated when the oxygen technique is used for measuring the rate of photosynthesis, mostly must be considered about 25 per cent. too high if a CO_2/O_2 exchange factor of 1 is used – as done by Gessner.

Theoretically, chlorophyll concentration would not seem to be very suitable for measuring the standing crop of phytoplankton. The chlorophyll concentration is first of all a factor of importance at low light intensities; cf. GABRIELSEN 1948. It has, however, been shown from many sides (e.g. by GESSNER 1944) that the amount of chlorophyll mostly – but not always – presents a relatively good measure of the standing crop of autotrophic algae. A high correlation is mostly found between the rate of photosynthesis at optimum light intensity and the concentration of chlorophyll.

During a cruise of the German Research ship "Südfall", Institut für Meeresforschung Kiel, in Danish waters in April 1956 chlorophyll measurements were made by Professor J. Krey in 24 water samples taken at a number of stations. At the same time the optimum rate of photosynthesis was measured in the same water samples by the senior author. The carbon-14 technique was employed, a water bath and optimum illumination being used. The assimilation number was normally about 5-8. A considerably lower assimilation number was found for certain water samples from relatively great depths, where the concentration of chlorophyll was extraordinarily high, in all probability due to the presence of "dead" chlorophyll, i.e. chlorophyll outside living cells.

Dr. R. W. Holmes, Scripps Institution of Oceanography, University of California, has kindly allowed us to quote some simultaneous measurements on chlorophyll a and organic production from the Pacific Ocean. The carbon-14 technique was employed. Surface water samples were trailed astern of the vessel from sunrise to noon. In the oligotrophic eastern part of the North Pacific Gyral observations were made at three stations:

Station No.	In situ production, mg.C/m.³/day	Computed optimum rate of production, mg.C/m.³/hour	Chlorophyll a, mg./m.³	Assimilation number
TransPac 6	1.12	0.25	0.168	5.4
– – 7	0.58	0.13	0.143	3.3
– – 12	0.68	0.15	0.102	5.4

The rates of production were practically the same as found by the "Galathea" in the same area. The position of St. TransPac 6 was 36°09.2′N, 133°20′W, that of St. TransPac 7 36°21.8′N, 134°53′W and that of St. TransPac 12 40°26.9′N, 143°32′W.

The assimilation number – i. e. mg. CO_2/mg. total chlorophyll per hour at optimum light intensity – is very near to those presented both for eutrophic and oligotrophic lakes; cf. i. a. GESSNER 1944. They are also near to those found in Danish Waters.

The concentration of chlorophyll in the photosynthetic layer in the oceans seems to vary between about 20 and about 0.1 mg./m.^{3} or a little less. When the concentration is highest the depth of the photosynthetic layer is only about $^1/_{10}$ of the depht found when the concentration of chlorophyll is very low. If the assimilation number always was the same, we would expect the rate of production to be about 20 times higher in the most eutrophic areas of the oceans compared with that in the really oligotrophic areas. According to the measurements made during the "Galathea" Expedition the organic production per surface unit was about 40 times higher in the most productive areas compared with the most unproductive areas of the oceans.

If using chlorophyll for estimating the standing crop of autotrophic algae, it must always be kept in mind that a considerable part of the chlorophyll possibly may be "dead". It seems rather likely that this normally is the case in the water masses below the photosynthetic zone. But it may be true even in surface water. At Georges Bank off the Atlantic coast of U.S.A. RILEY 1941 thus in June at St. 3961 found a O_2-production at the surface of 1.12 g./m.^{3} per day. The chlorophyll concentration was 7.0 mg./m.^{3}. At the same concentration (6.4 mg./m.^{3}) at St. 3965, also from June, the O_2-production was only 0.04 g./m.^{3}.

H. STANDING CROP OF ZOOPLANKTON AND ORGANIC PRODUCTIVITY

The zooplankton measurements in the South Atlantic – counts of metazoa in 4 1. samples – by the "Meteor" Expedition gave a distributional picture practically identical with that obtained by the phytoplankton counts – HENTSCHEL 1933. In Fig. 20, p. 78, Hentschels counts of metazoa and algae in the South Atlantic (0-50 m) are shown side by side. In the same figure the organic production per m^2 surface, the phosphate concentration and the colour of the sea are presented. In all instances the same distribution is observed. The plankton volumes from the "Dana" Expedition (JESPERSEN 1935), similarly show a striking resemblance to the measurements of productivity obtained during the cruise of the "Galathea", for the areas visited by both expeditions – cf. p. 86 and below. As the production of zooplankton must be more or less dependent on the amount of food – i.e., the phytoplankton production – this relation is quite obvious.

It is apposite to compare the present measurements of organic production at the longitudinal section in the Pacific from Samoa to Hawaii with the measurements of zooplankton volumina made by the Fish and Wildlife Service, Hawaii – KING 1954. For the phytoplankton, the correlation between the standing crop and the production is high – as shown in the section above. For the standing crop of zooplankton we must therefore expect a high correlation with both the standing crop and the production of phytoplankton.

Under special circumstances an inverted relation between quantities of phytoplankton and zooplankton may be found. At the very start of a phytoplankton bloom during spring in northern waters this seems to be normal, as the zooplankton production is delayed compared to that of the phytoplankton – STEEMANN NIELSEN 1937. Further under unstable conditions due e.g., to a concentration of zooplankton caused by currents or to the start of the dark season at higher latitudes, such an inverted relation undoubtedly occasionally may be found. Overgrazing in the sense of HARVEY *et al.* 1935 should thus be the reason for the poverty of phytoplankton, although probably many – but not all – of the cases given in the literature are artefacts only, due to the use of nets for measuring the phytoplankton crops, a method which is often very inadequate or even completely misleading – cf. GESSNER'S (1944) criticism. In coastal waters huge localised quantities of plankton larvae of bottom animals occasionally may be found decimating the crop of plankton algae – STEEMANN NIELSEN 1951. Animal exclusion in the sense of HARDY 1936 may or may not sometimes be of importance. It must also be mentioned here that practically all the observations used for demonstrating animal exclusion are based on investigations employing nets for measuring phytoplankton quantities. Normally, animal exclusion probably is of no importance at all. An inverted relation between quantities of phytoplankton and zooplankton is the exception. As a rule a very clear direct relation is found if adequate sampling techniques are used such as shown for the open ocean by Hentschel.

In the early plankton literature, there was a severe controversy between those regarding oceanic plankton to be patchy in its distribution and those regarding it to be relatively evenly distributed. Hentschel's results on the "Meteor" finally proved the latter theory to be true regarding the phytoplankton in the Tropics and Subtropics. Hardy 1936c on the other hand, has given some evidence that the opposite view holds for the zooplankton.

Although the total amount of grazers does not seem to show any pronounced patchiness, as shown by Hentschel 1933, Abb. 46, the local occurence of species and age groups very likely is subject to fluctuations. Such fluctuations would be comparable with the seasonal fluctuations found by Fish 1954 in the Sargasso Sea.

If the relation between the standing crop of zooplankton and organic production is considered, it is important to include only areas which can be strictly compared. Oceanic areas may not be strictly comparable to coastal areas – cf. below.

In Jespersen's 1935 survey of the quantities of zooplankton from the "Dana" Expedition, only real oceanic stations, with a few exceptions, were included. It is thus possible to compare organic productivity and zooplankton volumes from all the parts of the oceans investigated by the "Dana" and the "Galathea".

Table 19.

Area	Volume in cc./per one hour haul (average) (50-300 m. wire)	g.C/m.^{2}/ day produced by algae	Zooplankton (cc./hour): phyto-plankton (g.C/m.^{2}/ day)
Sargasso Sea-Antilles Current	219	0.06	3.800
Indian Ocean off Africa 20°-35°S	240	0.14	1.700
Indian Ocean between Mombassa and Madagascar	389	0.16	2.400
Carribean Sea	424	0.17	2.500
Indian Ocean between Madagascar and Ceylon (Station 3924 and Station 3926 omitted)	455	0.20	2.300
North Atlantic off North Africa – 10°-25°N	1630	0.40	4.100

According to Jespersen, Fig. 27, and corresponding measurements by the "Galathea", the Table 19 is obtained. In the first column is given the mean volume of macroplankton per hour from horizontal hauls in the upper layers (50-300 m. wire, corresponding to depths from about 25-150 m.) using a 2 m. stramin net; in the second column is given the average production in g. C/m.^{2}/day according to the "Galathea" measurements. No volumes from hauls from the Pacific are included, as the "Dana" unfortunately used a $1^1/_2$ m. stramin net for all depths in this ocean, whereas a 2 m. net was used in the upper layers in the other oceans.

The areas are taken according to those used by Jespersen with the exception that the North-Atlantic area off Africa, instead of extending from 35°-10°S, extended only from 35°S-20°S. Two of the 17 "Dana" stations from the area between Madagascar and Ceylon are omitted. These stations – 3924 and 3926 – showed rather special conditions. Vast quantities of salps were locally found here.

Although certainly too few areas are treated, and in spite of the fact that the relative zooplankton volumes from horizontal hauls are far from being an ideal measure of zooplankton quantities, the interrelation is clear. A similar interrelation could have been shown using instead the volumes of horizontal hauls from deeper layers – 1000-5000 m. wire out, depth about 500-2500 m. A net with a diameter of $1^1/_2$ m. was used here. The volumes are thus not directly comparable with those from the upper layers where the diameter of the net was 2 m. It may be mentioned that the mean volume of the hauls from the deeper layers was 291 ml./hour in the very eutrophic area of the North Atlantic off North Africa and 68 ml./hour in the very oligotrophic Sargasso Sea (including the Antilles Current). The influence of the production of organic matter by the plankton algae is thus as conspicuous in the volume of zooplankton from the deeper layers as in those from the upper layers.

In Fig. 41, the "Galathea" measurements of organic production from the longitudinal Pacific section between Samoa and Hawaii (14°S-24°N) are compared with quantitative measurements on zooplankton given as cm.^{3} per 1000 m.^{3} made during a cruise of a research vessel from the Fish and Wildlife Service, Hawaii (King 1954). Two sections were made, one at 170°W, one at 160°W. The time of the year was February-March (1951). The "Galathea" made the section during March 1952. To the south, the "Galathea" section was identical with the 170°

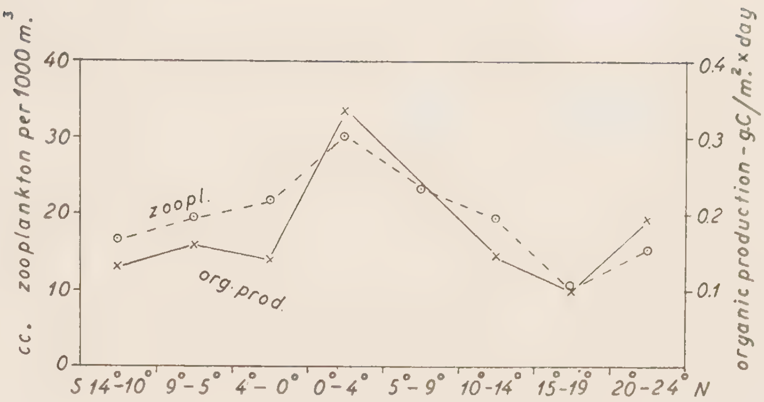

Fig. 41. Rate of organic production (Galathea) and volumn of zooplankton (after King 1954) on a longitudinal section across the Equator, 160°-170°W during February-March. All values given are averages for 5 degrees of longitude.

W-section, to the north with the 160°W-section. In comparing the zooplankton volumes with the organic production, the 170°W-section was used south of the Equator. Between Equator and 5°N the average of the two section was used and north of 5°N only the 160°W-section. The zooplankton material as used for the comparison consisted of altogether 64 hauls, distributed nearly evenly along the section. Averages for 5 latitudes were employed.

The two curves in Fig. 41 are very similar, both showing a pronounced maximum just north of the Equator coincident with the divergence near the southern boundary of the Counter Current.

In the section p. 110 dealing with grazing, the idea was put forward that the mean life of the grazers in the most oligotrophic areas probably must be considered to be somewhat longer than elsewhere. The cause should be due to the limited food supply resulting in a slower development. The relation of the standing crop of zooplankton to the organic matter produced by the algae should thus be relatively high in very oligotrophic areas (cf. last column in Table 19). If the Sargasso Sea (+ Antilles Current) area is compared with the three areas presented immediately below, some evidence for the hypothesis may be found. The ratio of the volume of zooplankton to the rate of organic production is also high (according to Table 19) for the truly eutrophic area off the coast of North Africa. It may be assumed that this high ratio is caused at least partly by the route of the "Dana" being further offshore than that of the "Galathea". According to Hentschel 1933, Beil. 1, the concentration of phytoplankton is decidedly higher here some hundred miles off the shore than nearer to the coast. A rather attractive object for future research should be the investigation of the relation between the standing crop of zooplankton and the organic production using more adequate methods.

Riley and Gorgy 1948 have estimated the zooplankton in the northwestern part of the Sargasso Sea from quantitative hauls between a depth of 400 m. and the surface as 1-2 g. dry weight below each m². This would seem to agree rather well with an estimate based on Hentschel's zooplankton counts in the most oligotrophic areas of the Atlantic. The phytoplankton standing crop per m.² surface may be estimated to be about 0.5 g. dry weight according to the measurements by the "Galathea" in the Sargasso Sea (– cf. p. 77). The weight of the standing crop of zooplankton being about 3 times the weight of phytoplankton seems to be rather adequate for a region of the present kind. The daily food available for the zooplankton corresponds to the net production of phytoplankton. As shown p. 77, it is 0.04 g. C = 0.15 g. dry weight. It represents about 10 per cent. of the dry weight of the zooplankton. As a minor part of the zooplankton is carnivorous the daily diet of the herbivorous plankton animals most likely must be a little more than 10 per cent. of their own body weight. Unfortunately we do not know how much of the assimilated food is used for respiration and how much for growth and reproduction in oligotrophic areas. If food is plentiful, it has been shown for copepods that by far the most of the assimilated organic matter is used for growth and reproduction. Experiments by Riley and Gorgy 1948 in the Sargasso Sea showed that immediately after capture a crustacean zooplankton looses about 12 per cent. daily. This would mean a loss of the same size as the daily intake of food. Such experimentally found values are, however, certainly too high for the conditions in the sea. Evidence shows that the crustaceans increase their rate of respiration when enclosed in experimental bottles.

If it is assumed that in extremely oligotrophic tropical areas at least 80 per cent. of the assimilated food in the herbivorous zooplankton is used for respiration, the average lifetime of such an animal would be about 50 days. This is undoubtedly a long time compared with the lifetime in more eutrophic areas at the same temperature. According to the literature survey by CUSHING 1955, the lifetime in the North Sea during spring is about 80 days for the relatively big copepod *Calanus finmarchicus*. There is, however, no reason to expect that lifetimes have to be short due to a high temperature. A high temrature may, e.g., be counteracted by a low concentration of some of the enzymes taking part in the processes going on in the cells of the animals.

According to the studies by FISH 1954 a life time of about 50 days for the Oithona species in the Sargasso Sea would seem rather appropiate. The genus Oithona includes the most abundant copepod species in this area.

In eutrophic areas the daily food of the zooplankton has been found to be considerably more than 10 per cent. of their own weight. Although the reproduction of the algae is faster here than in oligotrophic areas, the relation: weight of standing crop of zooplankton to weight of standing crop of phytoplankton, may thus be supposed to be lower than in oligotrophic areas.

It must be noted, however, that a considerable part of the organic matter in the phytoplankton in a eutrophic coastal area is not digested by the zooplankton but is either directly eaten by the bottom-living fauna or is contributed in the form of more or less undigested faecal pellets to the bottom. In the oligotrophic parts of the oceans such undigested pellets are hardly produced in any quantity by the zooplankton. With the exception of the minor part of algae lost by sinking into the abysses – cf. 110 – nearly all of the organic matter produced by the algae is presumably digested here by the zooplankton.

APPENDIX 1. THE INFLUENCE ON THE PRODUCTION RATE OF THE FILTRATION OF SEA WATER THROUGH FINEST BOLTING SILK

When at the beginning of this century Lohmann introduced the centrifuge for quantitative measurements of marine phytoplankton, he was able to show – see e.g. LOHMANN 1908 – that the fine silk net retained only a small part of the plankton algae. Despite this fact, silk nets have been used by many for estimating phytoplankton quantities and they are still in use in many countries. Warnings – such as by STEEMANN NIELSEN 1938 and by GESSNER 1944 – seem to have had only a very limited effect. It should indeed be unnecessary to give additional experimental evidence for the unsuitability of nets for quantitative phytoplankton estimations.

Some experiments on the effectiveness of nets were nevertheless made during the expedition. The reason for this was to provide a refutation of an argument often advanced by the workers still using nets; this argument is that although the bulk of the algae are lost through the nets, larger species retained are the main producers of organic matter.

As mentioned on p. 111, some special experiments were made at 56 stations during the latter part of the expedition. Surface water was used. One sub-sample was filtered through finest bolting silk (No. 25) before the start of the illumination, one was filtered in the same way after the end of the illumination and one was not filtered through the silk at all. The three samples were used for ordinary productivity measurements in the tank. They were illuminated for 4 hours. Whereas the difference between samples one and two theoretically should give information about the rate of grazing, the difference between samples 2 and 3 tells how much of the organic productivity is due to algae which are retained by the silk.

Fourteen coastal stations (depth less than 300 m.) gave an average photosynthetic rate of 82 per cent. of that of unfiltered samples if the water was filtered through bolting silk before being filtered by the membrane filter. The total variation was between 31 and 102 per cent. Only two stations from Milford Sound, New Zealand, showed a really important decrease after filtering through the bolting silk. If these two stations are omitted, the average rate of the filtered samples is 89 per cent. This means that net samples generally would have given values of about 10 per cent. of the real values.

Thirty six oceanic stations had an average photosynthetic rate of 94 per cent. if the water was filtered through bolting silk. The difference varied between 78 and 115 per cent. As the standard deviation for a single determination of a series of parallel determinations is about 6 per cent – cf. p. 62 – a difference between two parallel determinations amounting to more than 15 per cent. may be easily found.

Little stress need therefore be laid on the individual differences between the filtered and non-filtered samples. The average for the difference at all the stations must, on the other hand, be considered valid. Net samples from oceanic water must thus be supposed to give about 6 per cent. of the bio-mass of photosynthezising algae on the average. If the numbers of algae are determined instead, the difference between net samples and real quantitative samples is much higher. The big cells exclusively retained by the nets have a much higher rate of photosynthesis per cell than the average plankton algae found.

APPENDIX 2. AN ATTEMPT TO DETERMINE THE ORDER OF MAGNITUDE OF THE SINKING VELOCITY OF ALGAE, WITH INFORMATION ON THE RATE OF GRAZING AT THE DIFFERENT DEPTHS

By K. P. ANDERSEN

Let us assume that we have an ocean with a stationary number of algae per m.^{3}, and let this number A(z) be a function of the depth *z* alone. We assume further that the sinking velocity v m. per 24 hours is constant, that the organic production per m.^{3} 24 hours p(z), and the grazing per m.^{3} 24 hours g(z) are functions of z alone. The stationary condition makes it possible to find a relation between A(z), v, p(z) and g(z).

If we consider a water column with a cross section of 1 m.^{2} there will be A(z)dz algae between z and z + dz. During a time dt, $v \cdot A(z)\,dt$ algae will pass through a cross section at z, and vdt A(z + dz) will pass through at z + dz. During the same time dt we will have an organic production of p(z) dzdt and a grazing of g(z) dzdt between z and z + dz. This means that the number of algae between z and z + dz after a time dt will be:

$$A(z)\,dz + vA(z)\,dt - vA(z+dz)\,dt + p(z)\,dzdt - g(z)\,dzdt.$$

The stationary condition now gives:

$$A(z)\,dz = A(z)\,dz + vA(z)\,dt - vA(z+dz)\,dt + p(z)\,dzdt - g(z)\,dzdt$$

As $A(z+dz) = A(z) + A'(z)\,dz$ we get after dividing by dt:

$$p(z)\,dz - A'(z) \cdot v \cdot dz - g(z)\,dz = O \qquad (1)$$

Hentschels Data from the "Meteor" Expedition – cf. table 18 – give us some values of A(z):

$A(0) = 2.800 \cdot 10^6$
$A(50) = 3.600 \cdot 10^6$
$A(100) = 2.400 \cdot 10^6$
$A(200) = 0.287 \cdot 10^6$
$A(400) = 0.060 \cdot 10^6$
$A(700) = 0.016 \cdot 10^6$
$A(1000) = 0.013 \cdot 10^6$

From these figures and Fig. 41 in the present treatise corrected to net production it is possible to determine p (z) under the assumption that the total production per 24 hours in the productive layer (0-100 m.) is 25 % of the total number of algae in this layer.

In this way we find:

$p(0) = 0.82 \cdot 10^6$
$p(10) = 1.19 \cdot 10^6$
$p(20) = 1.42 \cdot 10^6$
$p(30) = 1.37 \cdot 10^6$
$p(40) = 1.17 \cdot 10^6$
$p(50) = 0.91 \cdot 10^6$
$p(60) = 0.63 \cdot 10^6$
$p(70) = 0.36 \cdot 10^6$
$p(80) = 0.20 \cdot 10^6$
$p(90) = 0.09 \cdot 10^6$
$p(100) = 0.00 \cdot 10^6$

(1) can be transformed to

$$\int_o^z p(z)\,dz - v \cdot A(z) - \int_o^z g(z)\,dz = 0 \qquad (2)$$

For $z \rightarrow o$ (2) gives

$v \cdot A(0) = 0$

As $A(0) \neq 0$ this means $v = 0$ at the surface. It is in this way clear that v cannot be independent of z. But it is probably not too far from reality to assume that v is independent of z for $z \geqq 30$ m. (1) is in this way only valid for $z \geqq 30$ m.

From the given A(z) it seems very reasonable to put $A(z) = A_{\text{max.}}$ for $z = 45$; this means $A'(45) = 0$ and (1) gives with $z = 40$ and $dz = 10$

$p(45) \cdot 10 - g(45) \cdot 10 = O$

or

$g(45) = p(45) = 1.04 \cdot 10^6$

To determine v it is necessary to make an assumption about g(z) and this assumption is very essential for the whole problem. We will assume that g(z) is constant from 40 m. to 60 m. We now put $z = 50$ and $dz = 10$ in (1) and get:

$$p(55) \cdot 10 - v \cdot \frac{A(100) - A(50)}{50} \cdot 10 - g(45) \cdot 10 = 0$$

or $0.77 \cdot 10^7 + 0.24 \cdot 10^6 - 1.04 \cdot 10^7 = 0$

and finally

$$v = 11 \text{ m/24 hours}$$

Having determined v it is now possible to estimate g(z).

(1) may written as

$$\int_{z_1}^{z_2} p(z)dz + A(z_1) \cdot v - A(z_2) \cdot v - \int_{z_1}^{z_2} g\,(z)dz = O$$

$z_1 = 50$ and $z_2 = 100$ gives:

$$\int_{50}^{100} g(z)dz = 30.9 \cdot 10^6 \qquad \text{mean } g(z) = 0.62 \cdot 10^6$$

$z_1 = 100$ and $z_2 = 200$ gives:

$$\int_{100}^{200} g(z)dz = 23.8 \cdot 10^6 \qquad \text{mean } g(z) = 0.24 \cdot 10^6$$

$z_1 = 200$ and $z_2 = 400$ gives:

$$\int_{200}^{400} g(z)dz = 2.5 \cdot 10^6 \qquad \text{mean } g(z) = 0.02 \cdot 10^6$$

For $z > 400$ we find $g(z) \simeq O$

As

$$\int_{0}^{1000} g(z)dz = \int_{0}^{1000} p(z)dz - v \cdot A(1000)$$

we have

$$\int_{0}^{50} g(z)dz = \int_{0}^{100} p(z)dz - v \cdot A(1000) - \int_{50}^{1000} g(z)dz = 19.6 \cdot 10^6$$

mean $g(z) = 0.40 \cdot 10^6$

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Table 20. The observations.

St No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
2	29.10.50	32°08′5 N	0	21.26	36.76		106	0.053	0.036
	Depth 4320 m.	14°00′ W	20	21.26	36.76			0.081	
			40	21.23	36.76			0.075	
3	29.10.50	31°17′ N	20	21.53	36.78		abt. 100	0.065	0.034
	Depth 4320 m.	14°20′ W							
4	2.11.50	21°30′0 N	0	19.93	36.40			9.10	
	Depth 62 m.	17°05′0 W	10	19.80	36.40		15	7.8	0.67
5	2.11.50	21°30′0 N	0	19.57	36.31		40	4.00	0.56
	Depth 62 m.	17°08′7 W	15	18.54	36.26			1.2	
6	3.11.50	18°20′5 N	0	26.83	35.03		abt. 60	1.9	0.55
	Depth 3000 m.	18°21′5 W	20	26.83	35.03		60	1.4	
			40	24.65	35.65			2.0	
7	3.11.50	17°10′2 N	0	26.84	35.08			0.64	
	Depth 3200 m.	18°30′0 W	20	26.33	35.35		62	0.61	0.24
			40	17.33	35.70			0.74	
11	7.11.50	14°30′0 N	0	27.33	34.60		51	0.72	
	Depth 94 m.	17°30′ W	20	21.77	35.59			0.70	0.20
			40	17.13	35.59			0.12	
12	7.11.50	14°08′5 N	0	27.67	34.97		47	0.39	
	Depth 1000 m.	17°46′ W	20	26.16	35.43			0.62	0.11
			40	18.26	35.61			0.55	
13	8.11.50	11°34′9 N	0	28.04	34.58			1.1	
	Depth 4750 m.	19°34′2 W	20	28.27	34.97		68	0.58	0.31
			40	20.91	35.53			0.88	
14	9.11.50	9°30′ N	0	27.81	34.83		84	1.1	0.46
	Depth 820 m.	17° 0′ W	20	27.71	34.92			1.1	
			40	23.43	35.53			0.89	
15	9.11.50	9°30′ N	0	28.25	33.73		63	1.4	
	Depth 290 m.	16° W	20	27.13	34.72			1.5	0.44
			40	20.59	35.55			0.96	
16	10.11.50	7°29′ N	0	28.44	31.20		65	1.1	
	Depth 340 m.	13°44′ W	90	15.83	35.57			0.24	0.41
20	13.11.50		0				28	10.00	0.77
	3 sm W off Monrovia, Liberia harbour								
	Depth 26 m.		8					2.6	
21	13.11.50		0					6.2	0.76
	500 m off entrance of Monrovia harbour		10				21	7.2	
	Depth 15 m.								
22	14.11.50	6°01′7 N	0	28.37	33.69	0.0	72	0.31	0.25
	Depth 220 m.	10°50′8 W	40	20.53	35.57	0.6		1.0	
			80	16.74	35.59	1.7		0.47	
23	14.11.50	5°31′0 N	0	27.88	34.40	0.1	79	0.44	
	Depth 2080 m.	10°42′0 W	40	19.90	35.66	1.0		1.6	0.36
			80	16.11	35.61	1.4		0.24	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
24	15.11.50	3°54′ N	0	27.41	34.67	0.0	45	0.31	
	Depth 3200 m.	8°22′ W	40	22.80	35.26	0.4		1.0	0.16
			80	17.09	35.66	1.7		0.14	
25	16.11.50.	2°06′ N	0	26.45	35.39	0.0		0.17	
	Depth 5050 m.	5°58′ W	40	24.83	35.64	0.0	65	0.59	0.12
			80	16.23	35.61	1.7		0.18	
28	17.11.50	1°47′5 N	0	26.19	35.48	0.2		0.16	
	Depth 5150 m.	5°49′5 W	40	25.16	35.59	0.0	68	0.67	0.15
			80	15.99	35.61	1.5		0.37	
30	18.11.50	0°42′ N	0	25.77	35.46	0.1		0.31	
	Depth 5160 m.	5°59′ W	40	25.43	35.48	0.2	75	1.2	0.35
			80	19.49	35.68	1.1		1.2	
31	19.11.50	1°56′ N	0	26.05	35.39	0.0		0.24	
	Depth 4930 m.	4°37′ W	40	24.84	35.46	0.0	81	0.77	0.22
			80	15.13	35.57	1.5		0.48	
32	20.11.50	4°05′ N	0	27.81	34.79	0.0		0.16	
	Depth 2100 m.	2°13′ W	40	26.93	35.07	0.0	89	0.45	0.14
			80	16.27	35.61	1.3		0.25	
40	25.11.50		1				6	10.5	0.34
	Anchorage Accra								
	Depth 7 m.								
43	26.11.50	5°37′ N	0	27.21	34.69	–	57	0.64	0.22
	Depth 30 m.	0°44′ E	20	27.28	34.74	–		0.78	
46	26.11.50	5°36′ N	0	28.44	34.63	0.1	28	0.36	
	Depth 280 m.	0°48′ E	15	27.13	34.72	0.1		1.6	0.21
			30	26.34	34.99	0.3		1.8	
47	27.11.50	2°54′ N	0	27.95	33.66	0.1	86	0.29	0.17
	Depth 4160 m.	3°50′ E	40	25.82	35.62	0.1		0.43	
49	29.11.50	0°00′	0	26.43	34.11	0.0	41	1.5	0.33
	Depth 42 m.	6°32′ E	10	26.47	34.22	0.0		1.5	
52	30.11.50	1°42′ N	0	26.54	28.12	0.0	61	1.6	
	Depth 2550 m.	7°51′ E	40	19.44	35.61	0.9		0.53	0.35
59	1.12.50	4°00′ N	0.5	28.04	19.13	–	6	22.0	
	Depth 9 m.	9°11′ E	5	26.18	30.88	–		8.3	0.49
63	2.12.50	2°00′ N	0	27.15	21.27	–	30	2.2	0.36
	Depth 1250 m.	9°14′ E	20	26.99	28.28			2.2	
			40	20.27	35.50			0.45	
64	3.12.50	0°16′ S	0	26.98	32.36	0.0	43	1.3	
	Depth 2240 m.	8°12′ E	20	26.30	33.96	0.2		1.7	0.28
			40	19.93	35.75	1.1		0.11	
65	4.12.50	2°17′ S	0	26.43	34.04	0.0	45	0.95	
	Depth 2610 m.	8°10′ E	20	24.83	34.94	0.1		1.9	0.36
			40	22.78	35.41	0.1		1.6	
66	5.12.50	4°00′ S	0	26.98	32.59	0.0	22	1.4	0.14
	Depth 4020 m.	8°25′ E	20	24.57	35.64	0.2		1.0	
			40	18.06	35.53	0.9		0.14	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.^{3} per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.^{2} in g. C. per day
67	6.12.50	5°00′ S	1	26.69	29.43	0.1	10	0.53	0.25
	Depth 2830 m.	9°15′ E	10	26.66	29.69	0.3		3.9	
68	6.12.50	5°19′ S	1	26.83	28.73	0.0	6	17.5	
	Depth 1840 m.	10°55′ E	10	26.10	30.93	0.4		8.6	0.57
71	7.12.50	5°23′ S	1	25.43	25.99	0.0	5	5.6	0.15
	Depth 880 m.	11°28′ E	10	25.36	34.83	0.3		4.6	
73	7.12.50	5°41′ S	1	25.33	23.93	0.0	4	4.2	
	Depth 430 m.	11°26′ E	10	25.25	34.94	0.2		4.7	0.08
82	8.12.50	5°53′ S	1	24.99	18.78			9.8	
	Depth 25 m.	12°04′ E	10	22.89	35.50	0.3	5	1.1	0.03
93	10.12.50	6°38′ S	0	25.74	34.27	0.0	50	1.4	
	Depth 685 m.	11°32′ E	20	25.63	34.42	0.1		2.3	0.45
			40	21.63	35.55	0.4		0.74	
95	10.12.50	6°51′ S	0	26.91	34.36	0.1	39	1.0	
	Depth 1120 m.	11°15′ E	20	26.34	34.49	0.1		1.8	0.30
			40	18.45	35.79	0.4		1.3	
97	10.12.50	8°22′ S	0	26.98	33.30	0.0	35	0.71	
	Depth 2680 m.	11°08′ E	20	22.95	35.81	0.4		3.2	0.36
			40	16.21	35.66	2.0		0.14	
98	10.12.50	8°52′ S	0	26.83	34.74	0.2	32	0.74	0.18
	Depth 2750 m.	11°09′ E	20	19.80	35.77	0.5		1.4	
			40	16.51	35.70	1.8		0.40	
101	12.12.50	8°50′ S	0	25.84	35.05	0.2	43	1.2	
	Depth 975 m.	12°32′ E	20	25.28	35.50	0.2		3.5	0.39
			40	19.80	35.62	1.1		5.9	
105	18.12.50	10°45′ S	0	25.63	36.06	0.1		0.29	0.21
	Depth 3980 m.	11° 3′ E	20	23.65	36.06	0.1	43	1.3	
			40	16.80	35.81	2.0		0.97	
106	18.12.50	11°24′ S	0	25.83	35.82	0.1	41	0.42	0.12
	Depth 3660 m.	11°15′ E	20	23.08	35.79	0.2		0.59	
			40	16.46	35.64	2.2		0.27	
109	19.12.50	12° 6′ S	0	26.99	34.94	0.2		0.57	
	Depth 1170 m.	13°08′ E	20	21.79	35.21	0.4		3.4	0.41
			40	18.36	35.64	1.7	38	1.04	
118 a	20.12.50	12°20′ S	0	24.5		0.4		5.4	
		13°40′ E	10	21.0		1.5	21	1.5	0.38
126	21.12.50	14°35′ S	0	24.03	35.55	0.3	34	1.6	
	Depth 1930 m.	12°06′ E	20	19.49	35.64	1.2		1.31	0.32
132	22.12.50	17°13′ S	0	16.77	35.52	1.7		18.0	1.92
	Depth 200 m.	11°27′ E	15	16.72	35.52	1.7		15.4	
			30	16.70	35.55	2.0	19	17.7	
136	22.12.50	17°13′ S	0	17.53	35.57	1.3		15.3	
	Depth 960 m.	11°12′ E	15	17.52	35.57	1.4	16	8.4	1.23
138	24.12.50	22°45′ S	0	15.73	35.05	1.7		7.5	
	Depth 80 m.	14°15′ E	15	12.48	35.10	2.4	39	0.92	0.85
			30	12.20	35.08	2.4		0.16	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.^{3} per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.^{2} in g. C. per day
139	24.12.50	Walvis Bay	0	19.80	35.26	2.2	0.8	780	abt. 3.8
	Depth 6 m.								
143	25.12.50	23°16′ S	0	15.43	35.03	1.7	37	3.5	
	Depth 150 m.	14°02′ E	15	13.73	35.01	1.7		1.1	0.46
			30	12.63	35.05	2.2		0.47	
153	27.12.50	29°00′ S	0	16.74	34.97	0.4		3.0	
	Depth 182 m.	15°29′ E	15	16.73	34.96	0.4	27	3.1	0.53
154	28.12.50	32°37′ S	0	13.48	34.88	0.2		22	
	Depth 255 m.	17°25′ E	15	12.63	34.94	0.4	11	26	1.8
159	2.1.51.	33°58′ S	0	10.61	34.76	1.1	40		1.4
	Depth 100 m.	18°09′ E							
167	3.1.51	34°16′ S	0	15.45	35.19	0.7		22	
	Depth 50 m.	18°32′ E	15	15.36	35.17	0.4	18	19	2.5
169	3.1.51	34°11′ S	0	18.3	–	–		3.7	
	Depth 20 m.	18°27′ E	15		–	–	20	3.1	0.46
175	21.1.51	35°00′ S	0	21.46	35.61	0.2		0.27	
	Depth 4330 m.	27°22′ E	40	21.17	35.59	0.1		0.41	
			80	19.97	35.57	1.7	81	0.97	0.24
178	23.1.51	35°07′ S	0	21.94	35.64	0.2		0.22	
	Depth 4630 m.	30°35′ E	40	21.10	35.64	0.2		0.21	
			80	19.98	35.57	0.3	101	0.16	0.13
180	25.1.51	34°56′ S	0	21.27	35.57	0.2		0.25	0.11
	Depth 5220 m.	36°31′ E	40	19.71	35.57	0.1		0.21	
			80	18.60	35.59	0.3	80	0.17	
181	26.1.51	34°54′ S	0	22.09	35.73	0.1	92	0.17	
	Depth 5380 m.	38°02′ E	40	20.96	35.73	0.1		0.14	
			80	19.30	35.68	0.1		0.21	0.1
184	29.1.51	33°06′ S	0	23.60	35.50	0.1		0.35	
	Depth 1470 m.	35°21′ E	80	21.74	35.52	0.1	94	0.32	0.2
185	30.1.51	32°31′ S	0	22.72	35.55	0.2		0.35	
	Depth 1680 m.	35°01′ E	40	22.72	35.53	0.2	85	0.30	0.17
186	31.1.51	32°33′ E	0	23.53	35.55	0.2	79	0.31	0.17
	Depth 3620 m.	32°01′ E	40	23.02	35.55	0.2		0.36	
			80	21.00	35.53	0.5		0.33	
191	4.2.51	31°49′ S	0	23.30	35.48	0.1		0.22	
	Depth 3510 m.	32°52′ E	40	22.93	35.52	0.1	96	0.22	0.14
			80	21.22	35.44	0.3		0.24	
197	14.2.51	29°57′ S	0	24.39	35.44	0.1	30	5.5	0.73
	Depth 605 m.	31°26′ E	20	23.10	35.37	0.2		3.2	
			40	21.15	35.34	0.7		3.2	
198	15.2.51	30°32′ S	0	24.63	35.55	0.2	86	0.2	0.11
	Depth 2690 m.	34°27′ E	40	24.20	35.55	0.2		0.21	
			80	20.30	35.50	0.2		0.28	
200	17.2.51	29°39′ S	0	24.58	35.59	0.1	105	0.18	0.12
	Depth 5050 m.	37°01′ E	40	23.16	35.57	0.1		0.19	
			80	20.00	35.50	0.2		0.24	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate μg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.^{3} per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.^{2} in g. C. per day
201	20.2.51	28°04′ S	0	27.08	35.48	0.2	101	0.36	0.23
	Depth 2110 m.	35°25′ E	40	26.00	35.55	0.2		0.42	
			80	22.21	35.41	0.2			
206	24.2.51	20°01′ S	0	28.45	35.82	0.0	23	4.4	0.59
	Depth 30 m.	35°10′ E	15	28.40	35.82	0.0		4.2	
209	24.2.51	20°08′ S	0	29.15	35.35	0.2	72	1.1	0.43
	Depth 75 m.	35°33′ E	30	26.65	35.41	0.2		1.3	
			60	19.00	35.32	0.9		0.32	
216	26.2.51	16°24′ S	0	27.77	34.34	0.2	102	0.51	0.24
	Depth 2760 m.	42°29′ E	40	28.10	34.81	0.2		0.35	
218	28.2.51	13°41′ S	0	27.47	34.25	0.1	83	0.32	0.13
	Depth 3300 m.	46°40′ E	40	26.93	34.99	0.2		0.33	
			80	22.23	35.28	0.3		0.11	
228	5.3.51	9°31′ S	0	28.48	34.92	0.2	91	0.30	0.23
	Depth 5050 m.	49°29′ E	40	26.34	34.97	0.0		0.64	
			80	21.14	35.21	0.0		0.44	
230	7.3.51	9°02′ S	0	29.16	34.92	0.2	87	0.28	0.22
	Depth 4950 m.	49°27′ E	40	26.39	35.21	0.3		0.77	
			80	19.30	35.23	1.1		0.2	
234	10.3.51	5°25′ S	0	29.21	35.50	0.3	101	0.25	0.13
	Depth 4830 m.	47°09′ E	40	25.70	35.34	0.3		0.31	
			80	18.60	35.32	1.3		0.63	
238	13.3.51	3°23′ S	0				87	0.3	
	Depth 3970 m.	44°04′ E	40					0.32	0.14
262	23.3.51	4°16′ S	0	28.02	35.55	0.3		0.31	
	Depth 2720 m.	41°33′ E	40	26.56	35.59	0.3	88	0.61	0.21
			80	25.59	35.64	0.4		0.3	
263	24.3.51	4°14′ S	0	29.90	35.34	0.2	86	0.33	0.15
	Depth 4650 m.	44°52′ E	80	24.90	35.59	0.4		0.33	
264	25.3.51	3°12′ S	0	30.27	35.28	0.2	90	0.35	abt. 0.19
	Depth 4920 m.	47°01′ E	40	27.50	35.35	0.2		0.52	
			80	19.38	35.32	0.9			
265	26.3.51	3°30′ S	0	30.63	35.53	0.2	87	0.21	0.15
	Depth 5340 m.	50°20′ E	40	27.90	35.44	0.2		0.34	
			80	26.02	35.44	0.2		0.52	
266	27.3.51	3°38′ S	0	29.72	35.30	0.2	86	0.26	0.15
	Depth 4720 m.	52°43′ E	40	27.45	35.35	0.3		0.39	
			80	24.41	35.39	0.4		0.24	
267	28.3.51	3°07′ S	0	30.15	35.32	0.3	85	0.23	
	Depth 4150 m.	54°09′ E	40	27.00	35.39	0.3		0.45	0.14
			80	19.75	35.32	0.3		0.12	
272	2.4.51	3°20′ S	0	29.30	35.41	0.4	88	0.28	0.20
	Depth 4110 m.	57°16′ E	40	28.81	35.46	0.3		0.62	
			80	25.24	35.44	0.3		0.32	
273	3.4.51	2°54′ S	0	29.20	35.35	0.4	107	0.24	0.23
	Depth 4320 m.	60°26′ E	40	29.07	35.41	0.4		0.48	
			80	28.31	35.46	0.3		0.49	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate μg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per $m.^3$ per hour at 18.000 Lux (correct temperature)	Organic gross production below one $m.^2$ in g. C. per day
274	4.4.51	2°04′ S	0	29.10	35.25	0.4		0.24	0.24
	Depth 4485 m.	64°00′ E	40	28.55	35.41	0.3		0.67	
			80	24.30	35.39	0.5	94	0.50	
275	5.4.51	1°15′ S	0	28.72	35.19		93	0.48	0.24
	Depth 2410 m.	67°25′ E	40	28.58	35.23			0.51	
			80	24.91	35.48			0.38	
276	6.4.51	0°42′ S	0	29.38	35.14	0.3	92	0.24	0.22
	Depth 4630 m.	71°07′ E	40	28.59	35.16	0.3		0.60	
			80	24.96	35.52	0.5		0.52	
278	7.4.51	0°10′ S	0	29.03	35.05	0.3	94	0.17	0.16
	Depth 2640 m.	74°02′ E	40	28.29	35.14	0.2		0.38	
			80	24.75	35.46	0.5		0.46	
279	8.4.51	1°00′ N	0	28.75	34.69	0.3		0.22	
	Depth 4300 m.	76°17′ E	40	28.62	35.03	0.3	94	0.29	0.14
			80	24.08	35.48	0.9		0.29	
281	10.4.51	3°38′ N	0	29.51	34.72		92	0.22	0.15
	Depth 3400 m.	78°15′ E	40	29.26	34.97			0.26	
			80	28.40	35.17			0.56	
282	11.4.51	5°32′ N	0	29.70	34.25	0.3		0.23	
	Depth 4040 m.	78°41′ E	40	28.58	34.67	0.3	86	0.62	0.19
			80	25.56	34.69			0.23	
283	12.4.51	7°05′ N	10	29.55	34.05	0.2	85	0.94	0.47
	Depth 820 m.	79°37′ E							
286	20.4.51	7°50′ N	0	29.70	34.16	0.2	60	1.8	0.41
	Depth 28 m.	81°43′ E	10	28.77	34.27	0.2		1.0	
			20	28.28	34.20	0.2		0.6	
298	23.4.51	14°20′ N	0	29.40	33.75	0.1	66	0.29	0.12
	Depth 3240 m.	82°00′ E	40	28.12	33.91	0.2		0.40	
			80	26.67	34.40	+		0.25	
299	24.4.51	17°10′ N	0	28.52	33.96	0.2	45	1.2	0.25
	Depth 2860 m.	84°30′ E	20	24.70	34.70	1.3		0.87	
			40	18.29	34.90	3.2		0.52	
303	26.4.51	20°37′ N	0	27.28	34.02		51	1.9	0.6
	Depth 62 m.	87°33′ E	20	27.10	34.00			2.2	
			40	25.48	34.29			2.7	
313	2.5.51	19°53′ N	0	29.20	32 65	0.0	84	0.37	0.16
	Depth 1400 m.	89°05′ E	40	27.53	33.28	0.0		0.38	
			80	24.47	34.63	1.7		0.27	
315	4.5.51	13°58′ N	0	30.19	32.54	0.1	99	0.31	0.24
	Depth 3000 m.	91°03′ E	40	28.12	33.62	0.2		0.55	
			80	25.61	34.20	0.4		0.50	
317	5.5.51	10°32′ N	0	29.89	32.66	0.2	85	0.55	0.31
	Depth 850 m.	90°59′ E	40	29.22	32.99	0.2		0.89	
			80	22.49	34.40	2.0		0.42	
325	10.5.51	4°20′ N	0	30.17	30.72	0.0	36	3.6	0.53
	Depth 46 m.	98°54′ E	20	29.90	31.24	0.1		2.0	
			40	29.32	32.56	0.3		2.1	

St No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
327	11.5.51	1°55′ N	0	30.16	30.73	0.2	19	6.2	0.52
	Depth 45 m.	102°27′ E	10	30.05	30,75	0.2		4.7	
			20	30.04	30.72	0.2		3.5	
372	6.6.51	3°48′ N	0	29.30	32.72	0.2	50	1.6	0.53
	Depth 25 m.	103°40′ E	10	28.79	32.74	0.2		2.0	
			20	28.77	32.72	0.2		2.3	
381	8.6.51	7°0′ N	10	30.08	31.51		60	2.2	abt. 0.7
	Depth 54 m.	103°18′ E							
382	9.6.51	7°57′ N	0	30.30	31.40	0.0	69	0.73	0.49
	Depth 78 m.	102°32′ E	40	28.87	31.73	0.2		2.0	
			68	26.91	33.08	0.7		1.0	
384	10.6.51	10°11′ N	0	29.73	31.51	0.1	64	2.0	0.78
	Depth 72 m.	101°37′ E	30	29.40	31.67	0.2		1.7	
			68	27.40	32.86	1.4		3.6	
390	11.6.51	13°02′ N	0	29.82	31.78		31	6.0	1.08
	Depth 22 m.	100°33′ E	10	29.82	31.74			7.1	
			20	29.82	31.73			5.0	
408	4.7.51	12°56′ N					abt. 100	0.28	abt. 0.16
	Depth 4330 m.	116°11′5 E							
409	5.7.51	13°44′ N	0	28.88	33.08	0.9	98	0.15	0.15
	Depth 3780 m.	118°56′ E	50	28.92	33.35	0.2		0.42	
			100	23.03	34.29	0.2		1.1	
411a	11.7.51	12°41′ N							
		123°27′ E						0.098	
412a	12.7.51	11°38′ N					abt. 120	0.15	0.1
		126°11′ E							
414	17.7.51	10°20′ N	0	28.03	34.34	+	56	2.6	0.8
	Depth 40 m.	125°32′ E	15	28.02	34.33	0.1		2.2	
			30	27.84	34.34	0.1		2.5	
422	24.7.51	10°47′ N	0	29.95	34.34	0.4	118	0.12	0.11
	Depth 2150 m.	126°02′ E	60	28.75	34.36	0.3		0.21	
435	8.8.51	10°20′ N	0	29.19		0.5	119	0.10	0.08
	Depth 9790 m.	126°41′ E	60	28.28		0.3		0.14	
			120	25.62		0.4		0.15	
443a	17.8.51	8°22′8 N					abt. 90	0.43	0.21
		122°26′4 E							
447	20.8.51	3°05′ N	0	30.00	34.04	0.1	90	0.37	0.14
	Depth 4660 m.	120°10′ E	50	27.61	34.47	0.2		0.24	
			100	23.80	34.79	0.4		0.17	
454	25.8.51	5°23′ S	0	27.79	34.18	0.0	63	1.8	0.59
	Depth 60 m.	116°02′ E	25	27.65	34.04	0.0		1.5	
			50	25.11	34.04	0.7		2.1	
456	26.8.51	5°00′ S	0	28.08	33.46	0.1	50	0.9	0.32
	Depth 60 m.	111°11′ E	25	27.83	33.75	0.1		1.3	
			50	27.74	33.86	0.1		1.5	
458	27.8.51	6°08′ S	0	28.25	31.18	0.1	21	1.9	0.23
	Depth 20 m.	107°57′ E	15	27.73	31.09	0.1		2.2	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.^{3} per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.^{2} in g. C. per day
466	6.9.51	10°21′ S	0	26.09	34.34	0.2	59	0.43	0.17
	Depth 7130 m.	110°12′ E	34	25.85	34.34	0.1		0.53	
			60	25.48	34.36	0.2		0.64	
472	10.9.51	10°24′ S	0	25.29	23.23	0.1	34	3.7	0.7
	Depth 2470 m.	114°07′ E	15	24.60	34.23	0.2		4.3	
			30	23.44	34.27	0.4		2.9	
475	11.9.51	9°02′ S	0	25.60	34.14	0.2	40	3.4	0.59
	Depth 2750 m.	114°48′ E	15	25.58	34.14	0.2		2.7	
			30	24.40	34.16	0.3		1.3	
491 a	17.9.51	5°45′ N					abt. 60	0.63	abt. 0.2
		119°59′ E							
491 b	19.9.51	6°16′5 S					abt. 50	1.2	abt. 0.3
		129°05′ E							
498	24.9.51	5°18′ S	0	26.68	34.60	0.3	42	1.8	0.34
	Depth 7280 m.	131°06′ E	30	26.30	34.59	0.4		1.6	
			60	23.11	34.52	1.3		0.66	
511 a	4.10.51	11°42′ S					abt. 80	0.43	0.18
		152°16.5′E							
515 a	10.10.51	7°47′ S					abt. 80	0.73	0.31
		155°40.5′E							
517	12.10.51	6°31′ S	0	28.09	34.69	0.4	80	0.56	0.29
	Depth 8920 m.	153°58′ E	40	28.22	34.63	0.4		0.53	0.25
			80	28.05	35.23	0.5		0.67	
				+					
518	14.10.51	6°11′ S					abt. 100	0.21	0.11
	Depth 8860 m.	153°31′ E							
519 a	16.10.51	5°59′ S					abt. 100	0.30	0.16
		153°27′ E							
522	18.10.51	11°27′ S	0	27.22	35.17	0.3	83	0.40	0.19
	Depth 2600 m.	151°48′ E	40	26.25	35.16	0.4		0.53	
			80	25.10	35.16	0.4		0.33	
523	19.10.51	9°35′ S	0	25.75	35.08	0.2	94	0.18	0.12
	Depth 1200 m.	147°05′ E	50	25.30	35.12	0.2		0.21	
			100	24.95	35.17	0.3		0.39	
538	5.11.51	26°27′ S	0	22.44	35.48	0.3	63	0.44	0.19
	Depth 55 m.	153°27′ E	20	22.20	35.48	0.3		0.65	
			40	22.19	35.48	0.3		0.44	
550	12.11.51	31°27′ S	0	21.24	35.61		63	0.37	0.15
	Depth 4410 m.	153°33′ E	40	20.80	35.57			0.26	
			80	20.20	35.62			0.56	
553	4.12.51	39°03′ S	0	14.75	35.39	0.1	62	0.78	0.42
	Depth 84 m.	144°04′ E	30	14.00	35.39	0.2		0.99	
			60	13.94	35.39	0.2		1.5	
564	6.12.51	36°18′ S	0	18.34	35.71	0.1	83	0.36	0.15
	Depth 60 m.	138°29′ E	25	16.21	35.68	0.1		0.22	
			50	15.45	35.75	0.1		0.25	

St No.	Date	Position	Depth of sample in m.	Tempe-rature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photo-synthetic layer in m.	Organic gross pro-duction in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross pro-duction below one m.² in g. C. per day
573	17.12.51	39°00′ S	0	17.53	35.55	0.2	abt. 60	1.3	
	Depth 4500 m.	154°57′ E	30	17.30	35.55	0.1		2.2	0.67
			60	16.64	35.52	0.1		1.2	
576	21.12.51	40°31′ S	0	15.44	34.65	0.2	28	12.0	1.94
	Depth 60 m.	173°20′ E	15	15.33	34.69	0.3		12.0	
			30	12.21	35.07	1.1		2.8	
580	3.1.52	52°33′ S	0	8.90	abt. 34.18	1.3		8.3	
	Depth 30 m.	169°08′ E	20	8.39	34.25	1.3	28	1.1	1.0
593	4.1.52	52°35′ S	0	8.59	34.31	1.3	62	1.3	0.55
	Depth 110 m.	169°14′ E	25	8.39	34.29	1.3		1.1	
			50	8.33	34.41	1.3		0.97	
599a	13.1.52	45°58′ S					abt. 55	0.55	0.21
		165°10′ E							
601	14.1.52	45°51′ S	0	12.71	34.81	1.3	55	1.1	0.43
	Depth 4400 m.	164°32′ E	25	12.20	34.76	0.4		1.1	
			50	12.08	34.78	0.4		1.3	
603	16.1.52	44°37′ S	0	14.84	20.59	0.1	18	6.2	1.48
	Depth 30 m.	167°55′ E	15	12.45	33.26	0.4		17.9	
615	19.1.52	44°37′ S	0	13.34	16.65	0.0	24	10.7	1.89
	Depth 293 m.	167°53′ E	10	12.92	33.26	0.1		7.8	
			20	12.68	33.96	0.1		20.5	
625	20.1.52	42°08′ S	0	15.85	33.05	0.3	63	0.26	0.23
	Depth 595 m.	170°20′ E	25	14.94	35.04	0.3		0.67	
			50	14.31	35.06	0.3		0.76	
630	25.1.52	39°45′ S	0	18.28	35.21	0.1	64	0.28	0.31
	Depth 320 m.	177°41′ E	30	17.43	35.31	0.1		0.84	
			60	15.76	35.33	0.3		1.6	
637	26.1.52	37°28′ S	0	18.63	35.25	0.1	55	1.7	0.54
	Depth 1400 m.	178°18′ E	25	18.29	35.27	0.2		1.4	
			50	16.58	35.35	0.4		1.6	
641	27.1.52	36°34′ S	0	19.00	35.21	0.2	51	2.3	0.62
	Depth 45 m.	174°59′ E	20	18.90	35.24	0.2		2.3	
			40	14.79	35.19	1.3		1.8	
669	29.2.52	36°10′ S	0	21.28	35.50	0.2	97	0.17	0.14
	Depth 2490 m.	177°50′ E	40	20.58	35.58	0.2		0.26	
			80	17.85	35.53	0.3		0.44	
670	1.3.52	34°07′ S	0	21.75	35.34	0.1	82	0.22	0.10
	Depth 4000 m.	179°20′ W	40	19.76	35.41	0.2		0.33	
			80	15.93	35.44	0.7		0.065	
677	4.3.52	28°38′ S	0	24.02	35.64	0.1	106	0.26	0.13
	Depth 9190 m.	175°53′ W	50	abt. 22	35.58	0.1		0.21	
			100	17.92	35.55	0.2		0.16	
680	7.3.52	23°24′ S	0	27.17	35.03	0.1	102	0.22	0.11
	Depth 7800 m.	175°01′ W	60	25.30	35.23	0.1		0.21	
			120	22.28	35.32	0.2		0.17	
683a	9.3.52	21°12′ S						2.5	
		174°41′ W							

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.³ per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.² in g. C. per day
685	10.3.52	21°06′ S	0	26.51	35.53	0.2	95	0.31	0.16
	Depth 9820 m.	173°33′ W	60	26.36	35.61	0.2		0.27	
			120	24.30	35.63	0.2		0.39	
688	15.3.52	13°42′ S	0	29.60	35.28	0.3	120	0.19	0.10
	Depth 4720 m.	170°37′ W	60	28.07	36.04	0.3		0.17	
			120	25.00	36.22	0.3		0.077	
690	16.3.52	11°01′ S	0	29.58	34.99	0.2	120	0.19	0.16
	Depth 600 m.	171°07′ W	60	29.48	35.01	0.2		0.21	
			120	26.59	35.97	0.5		0.39	
691	17.3.52	6°00′ S	0	29.45	35.19	0.3	113	0.19	0.14
								(0.38)[1]	(0.17)
	Depth 5790 m.	169°17′ W	60	29.22	35.35	0.3		0.28	
			120	27.59	35.97	0.7		0.17	
692	18.3.52	2°47′ S	0	27.80	35.35	0.7	78	0.24	0.10
								(0.48)[1]	(0.14)
	Depth 5570 m.	167°41′ W	60	27.70	35.41	0.7		0.24	
			120	27.86	35.62	0.7		0.26	
692a	19.3.52	0°02′ S					80	0.95	abt. 0.4
		166°29′ W							
693	20.3.52	4°00′ N	0	28.02	35.08	0.4	81	0.60	0.26
	Depth 5260 m.	164°48′ W	40	27.80	35.08	0.4		0.62	
			80	27.63	35.10	0.4		0.51	
694	22.3.52	13°00′ N	0	26.30	34.40	0.2	85	0.32	0.14
		162°42′ W	50	26.21	34.45	0.2		0.28	
			100	26.18	34.42	0.2		0.34	
695	23.3.52	16°00′ N	0	24.74	34.40	0.2	100	0.18	0.10
		159°00′ W	50	24.19	34.63	0.2		0.18	
			100	24.11	34.69	0.2		0.21	
696	24.3.52	19°57′ N	0	24.02	34.83	0.1	101	0.20	0.10
		158°10′ W	60	23.95	34.82	0.1		0.18	
			120	23.57	35.01	0.1		0.17	
698	29.3.52	23°00′ N	0	22.63		0.2	105	0.31	0.19
	Depth 4700 m.	155°25′ W	60	22.50	35.16	0.1		0.34	
			120	22.50	35.12	0.1		0.39	
698a	31.3.52	26°52′ N					100	0.08	abt. 0.08
		148°32′ W							
699	3.4.52	33°37′ N	0	14.60	33.57	0.2	97	0.11	0.1
	Depth 5260 m.	134°53′ W	60	14.56	33.71	0.2		0.24	
			120	15.38	34.11	0.2		0.21	
700	4.4.52	35°45′ N	0	13.43	33.10	0.4	77	0.27	0.13
	Depth 4755 m.	129°10′ W	40	12.20	32.94	0.5		0.32	
			80	11.63	32.86	0.4		0.39	
701	5.4.52	37°16′ N	0	11.50	32.86	0.3	63	0.89	0.55
	Depth 4755 m.	124°36′ W	30	11.06	32.88	0.5		0.76	
			60	11.04	32.97	0.4		0.47	
705	22.4.52	32°50′ N	0	16.37	33.24	0.3	23	2.1	0.36
	Depth 16 m.	117°32′ W	10	15.41	33.28	0.4		3.3	

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[1] A mistake in recording seems to have been made. The value in brackets is most likely correct.

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate μg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.^{3} per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.^{2} in g. C. per day
707	24.4.52	26°00′ N	0	17.01	33.60	0.3	67	0.59	0.24
	Depth 1600 m.	113°31′ W	30	16.40	33.66	0.4		0.59	
			60	15.40	33.71	0.5		0.52	
708	25.4.52	22°50′ N	0	18.34	34.38	0.5	34	3.5	0.9
	Depth 800 m.	110°06′ W	25	17.15	34.31	1.0		7.7	
			50	14.21	34.18	2.4		0.25	
709	26.4.52	20°00′ N	0	23.53	34.81	0.4	55	0.59	0.21
	Depth 3600 m.	106°12′ W	25	20.30	34.63	0.8		0.86	
			50	17.03	34.56	2.3		0.28	
715	4.5.52	13°00′ N	0	29.62	34.16	0.2	80	0.73	0.27
	Depth 4600 m.	95°48′ W	40	21.22	34.42	2.6		0.71	
			80	13.91	34.85	2.6		0.012	
717	7.5.52	8°41′ N	0	29.10	33.48	0.3	52	0.63	0.26
	Depth 3310 m.	86°12′ W	25	23.20	34.33	1.3		1.4	
			50	18.79	34.81	2.6		0.46	
719a	10.5.52	6°52′ N					60	1.4	0.48
		79°30′ W							
720	11.5.52	5°36′ N	0	26.72	33.78	0.4	60	1.9	0.40
	Depth 3000 m.	79°31′ W	30	21.38	34.43	1.7		0.99	
			60	16.60	34.90	2.6		0.31	
723	12.5.52	6°00′ N					60	0.72	0.23
	Depth 3230 m.	79°54′ W							
755	22.5.52	11°52′ N	0	28.63	35.99	0.1	90	0.21	0.14
	Depth 3960 m.	77°41′ W	50	26.93	36.42	0.1		0.30	
			100	24.01	36.76	0.1		0.41	
756	24.5.52	15°00′ N	0	28.06	35.97	0.1	63	0.51	0.19
	Depth 4200 m.	71°06′ W	40	27.70	35.97	0.2		0.64	
			80	26.94	35.95	0.2		0.44	
757	30.5.52	18°33′ N	0	27.70	36.00	0.1	100	0.12	0.056
	Depth 960 m.	65°36′ W	50	25.93	36.31	0.1		0.085	
			100	24.20	36.78	0.1		0.098	
760	2.6.52	22°43′ N	0	26.87	36.09	0.1	119	0.079	0.075
	Depth 6170 m.	60°54′ W	60	24.82	36.55	0.1		0.17	
			120	22.51	36.89	0.1		0.067	
760a	3.6.52	24°23′ N					120	0.045	abt.0.03
		57°04′ W							
762	4.6.52	25°03′ N	0	26.00	36.92	0.1	108	0.059	0.043
	Depth 6200 m.	56°06′ W	60	22.79	36.74	0.1		0.064	
			120	21.14	36.74	0.1		0.12	
763	6.6.52	29°27′ N	0	22.22	36.64	0.1	94	0.091	0.058
	Depth 4700 m.	47°53′ W	60	20.13	36.62	0.1		0.15	
			120	18.57	36.49	0.1		0.079	
764	7.6.52	31°35′ N	0	22.71	36.94	0.1	121	0.057	0.048
	Depth 3730 m.	43°31′ W	60	21.46	36.96	0.1		0.069	
			120	19.82	36.74	0.1		0.11	
765	9.6.52	35°16′ N	0	21.13	36.24	0.1	76	0.16	0.16
	Depth abt. 2000 m.	33°50′ W	40	18.34	36.20	0.1		0.70	
			80	16.34	36.7	0.2		0.17	

St. No.	Date	Position	Depth of sample in m.	Temperature °C	S ‰	Phosphate µg-atoms P per litre	Depth of photosynthetic layer in m.	Organic gross production in mg. C per m.^{3} per hour at 18.000 Lux (correct temperature)	Organic gross production below one m.^{2} in g. C. per day
766	10. 6. 52	36°50′ N	0	19.90	36.29	0.0	87	0.11	0.11
	Depth 3200 m.	28°50′ W	50	17.15	36.17	0.1		0.43	
			100	16.07	36.11	0.2		0.10	
768	14. 6. 52	37°53′ N	0				92	0.25	0.11
	Depth 2030 m.	24°45′ W	40					0.20	
			80					0.18	
769	16. 6. 52	43°10′ N	0	17.32	35.73	0.1	44	0.89	0.25
	Depth 4450 m.	17°04′ W	20	17.23	35.71	0.1		0.71	
			40	14.90	35.71	0.1		1.2	
770	17. 6. 52	45°53′ N	0	17.00	35.64	0.1	60	0.67	0.26
	Depth 4900 m.	12°27′ W	30	15.00	35.62	0.1		0.73	
			60	12.10	35.62	0.4		0.61	
772	18. 6. 52	48°00′ N	0	15.31	35.29	0.1	41	1.22	0.33
	Depth 1520 m.	8°18′ W	20	15.00	35.59	0.2		1.4	
			40	13.25	35.59	0.3		1.1	
775	19. 6. 52	49°37′ N	0	14.70	35.17	0.1	49	1.4	0.47
	Depth 80 m.	4°35′ W	20	14.30	35.16	0.1		2.1	
			40	11.53	35.23	0.3		0.55	
780	25. 6. 52	51°10′ N	0	13.71	35.05	0.1		2.1	0.72
	Depth 44 m.	1°41′ E	15	13.70	34.97	0.1		2.3	
			30	13.70	34.97	0.1		2.1	
781	26. 6. 52	54°50′ N	0	12.13	34.63	0.1	45	0.56	0.20
	Depth 45 m.	4°28′ E	20	11.93	34.60	0.1		0.59	
			40	$< 8.$	34.67	0.3		0.53	
782	28. 6. 52	57°43′ N	0	12.40	33.24	0.1	34	2.2	0.71
	Depth 16 m.	10°11′ E	10	12.35	33.28	0.1		3.0	

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A RED WATER ORGANISM FROM WALVIS BAY

(*Gymnodinium galatheanum* n. sp.)

By TRYGVE BRAARUD
University of Oslo

During the Danish "Galathea"-expedition 1950-52 red water was observed in Walvis bay on 24 December 1950. A sample preserved with formalin was collected by Professor E. Steemann Nielsen and forwarded to me for examination.

The plankton consisted of several species, dinoflagellates, *Euglena,* naked and thecate ciliates, but one species outnumbered all the others, a species of *Gymnodinium* or *Gyrodinium.* Since it does not seem to agree with any of the known species, we are describing it as *Gymnodinium galatheanum* n. sp.

Diagnosis: Cells without plate structure, but with a periplasm which seems to be firm. In ventral view both the anterior and posterior parts are broadly rounded, being connected by an extremely broad cingulum, which has a displacement of about 2 times its width. The cingulum is deeply excavated. The sulcus seems to be extremely narrow and is connected with a well defined furrow on the anterior part of the cell. In ventral view this furrow produces an indentation in the contour at the apex, giving a similar impression as an apical pore in thecate species. The posterior part of the cell has different outlines in ventral and dorsal views. While in ventral view the outline is smooth, like that of the anterior part, in dorsal view an irregular protrusion is visible on the left side of the cell. In oblique dorsal view still another protrusion is visible, which is considerably shorter and narrower. The smaller protrusion

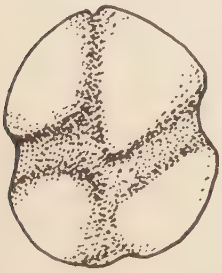

Fig. 1. *Gymnodinium galatheanum.* Sketch of cell in ventral view.

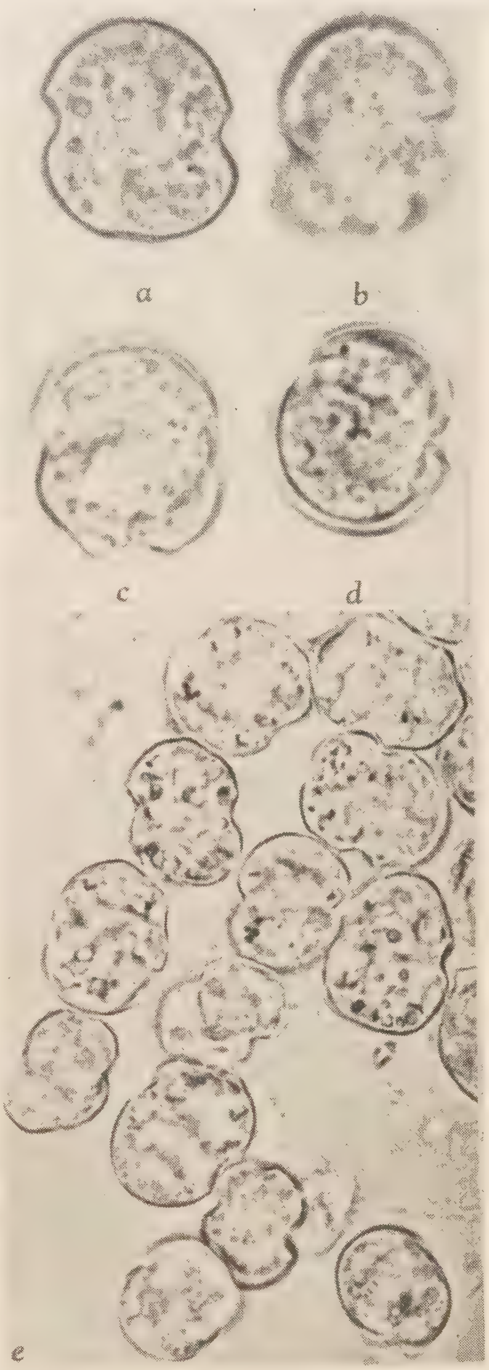

Fig. 2. *Gymnodinium galatheanum.* Photomicrographs of preserved material. a, in ventral view; b, in oblique side view; c, in oblique antapical view; d, optical cross section; e, part of the plankton sample, showing cells in various positions.

is due to a narrow fold, the larger represents a more rounded hump, both on the left side of the narrow sulcus. There are numerous rounded chromatophores.

Length of the cell: 14-17 μ, breadth: 10-14 μ.

The cells resemble *Gymnodinium boreale* GAARDER, but in that species neither the characteristic protrusions on the posterior part nor the pore-like indentation at the apex have been observed.

The displacement of the cingulum seems to be about $^1/_5$ of the length of the cell. This detail is, however, not easily seen and the species may just as well be referred to *Gyrodinium* as to *Gymnodinium*.

Trypan blue does not produce the blue characteristic of thecate dinoflagellates, and no signs of plates were observed. On the other hand the cingulum is clearly marked, even in preserved material, so a fairly firm periplasm seems to be present. During treatment with Eau de Javelle the cell content does not disappear until the outline of the cell becomes obscure.

The species which accompanied *Gymnodinium galatheanum* were mostly quite subordinate in numbers and have not been made the object of more detailed taxonomic studies. The list of forms which were observed is as follows:

Amphidinium sp.
Euglena sp.
Goniaulax sp.
Peridinium sp. (cf. *P. triquetrum)*
Ciliates, naked and thecate.

In comparison with *Gymnodinium galatheanum* they form a subordinate component of the plankton, and there is every reason to consider this species as the main cause of the red water observed on the date of sampling.

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DEEP-SEA BACTERIA

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SUMMARY[1]

The presence of living bacteria in some of the deepest parts of the ocean was demonstrated on the Galathea Expedition. Sediment samples taken from the bottom of the Philippine Trench at depths exceeding 10 000 meters were found to contain from 10^4 to 10^6 living bacteria per ml. Large bacterial populations were also detected in sediment samples from the floor of the Kermadec-Tonga Trench (6790 to 9820 meters), the Sunda Deep (7020 meters) in the Java Trough, and the Weber Deep (7250 meters) in the Banda Sea. Several hundred microbial analyses were made on nine sediment samples taken from depths exceeding 10 000 meters.

The occurrence of bacteria in deep-sea sediment samples was demonstrated by direct microscopic examinations shortly after the samples were hauled aboard the Galathea. Growth or reproduction of the bacteria in nutrient sea water media proved that the bacteria were alive. Their indigenity was indicated by three lines of evidence: (1) Every possible precaution was exercized to prevent the contamination of the deep-sea samples, (2) More bacteria were found in the sediment samples than in the overlying water, and (3) The deep-sea bacteria were unique in their ability to grow preferentially or exclusively at *in situ* hydrostatic pressures (700 to 1 000 atmospheres) and low temperatures (3 to 5°C).

Apparatus is described which was designed to maintain sediment samples and bacterial cultures at any desired pressure in the ship's refrigerator. This apparatus made it possible to send by Air Express deep-sea sediment samples held at 1 000 atm to our laboratory at Scripps Institution for further observation.

The deep-sea bacteria appear to be even more heat-sensitive than pressure-sensitive. Many were killed by holding them for ten minutes at 30°C. Less than 20 per cent of the deep-sea bacteria survived for ten minutes at 40°C.

The unique pressure, temperature, and nutrient requirements of the deep-sea bacteria presents an enigma in bacterial taxonomy, because the bacteria cannot be characterized by conventional or standard method cultural procedures. Morphologically the deep-sea bacteria resemble common soil and water forms, but physiologically and culturally they show differences which suggest that most deep-sea bacteria are new and undescribed species or genera.

Though predominantly aerobic, some of the deep-sea bacteria develop anaerobically. Among the physiological types that were present and active at *in situ* pressures and temperatures were starch hydrolyzers, nitrate reducers, sulfate reducers, ammonifiers, and nitrifiers. The types of bacteria present as well as the organic and sulfate content of profile series of mud cores from the Kermadec-Konga Trench suggests that the bacteria have been active *in situ* in altering organic compounds and in reducing sulfate.

Besides affecting the non-conservative chemical composition of sea water and sediment, the deep-sea bacteria are believed to contribute to the nutrition of benthic fauna. The "standing crop" of organic carbon in the cells of living bacteria is estimated at from 0.2 to 2.0 mg per liter of sediment at the mud-water interface. There may be from 10 to 100 "crops" or bacterial generations per year. The bacteria are believed to obtain their carbon and energy requirements from organic detritus settling to the sea floor and to a much larger extent from dissolved or colloidal organic compounds carried by the movements of water masses.

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[1] Contribution from the Scripps Institution of Oceanography, University of California, La Jolla, California, U.S.A., New Series No. 926. These investigations were supported in part by grants from the Office of Naval Research, U.S.A. Department of Navy, and the Rockefeller Foundation.

INTRODUCTION

Observations on the Galathea Expedition in 1951 demonstrated for the first time the occurrence of living bacteria in some of the deepest parts of the ocean. Prior to this time, 5942 meters was the greatest depth at which bacteria had been found. Most microbiologists questioned whether bacteria could exist in oceanic abysses, although an abundant microflora has been shown to occur in near-shore sediments (ZoBell, 1946).

On the Talisman Expedition, Certes (1884a) found a few bacteria in bottom deposits taken from a depth of 5100 meters. The indigenous nature of these bacteria was indicated by their ability to grow in nutrient medium at hydrostatic pressures that were approximately isobaric with the depth from which they were taken (Certes, 1884b). While on the Humboldt Plankton Expedition to the West Indies, Fischer (1894) found a few bacterial colonies on nutrient agar plates inoculated with deep-sea sediment samples, one of which came from a depth of 5280 meters, but there was nothing to indicate whether these bacteria were indigenous or adventitious species.

In 1948, we obtained from a 5800-meter deep off Bermuda a mud sample in which numerous barophilic bacteria were found. The term "barophilic" was coined by ZoBell and Johnson (1949) to characterize microbes which grow preferentially or exclusively at high hydrostatic pressures. During the 1950 Mid-Pacific Expedition to the Marshall Islands, large bacterial populations were demonstrated in pelagic sediments, including 14 samples taken from depths exceeding 4000 meters; one of these samples containing bacteria came from a depth of 5942 meters (Morita and ZoBell, 1955).

Cultural methods, supplemented by direct microscopic observations, were employed to investigate the numbers and kinds of bacteria in marine materials collected by the Galathea. Immediately after being hauled aboard the ship, deep-sea sediment and water samples were transferred aseptically to steel vessels for compression to hydrostatic pressures approximately isobaric with the depth from which taken, and placed in a refrigerator at 3-5°C. This operation ordinarily required from 5 to 15 minutes. Portions of each sample were removed for detailed examination as time and facilities permitted.

Temperature Tolerance of Deep-Sea Bacteria.

Haste in handling the deep-sea samples proved to be of utmost importance owing to the temperature sensitivity of the bacteria. About 25 per cent of the marine bacteria collected off the coast of California by ZoBell and Conn (1940) were killed in 10 minutes when warmed to 30°C and only 20 per cent survived for 10 minutes at 40°C. Deep-sea bacteria have proved to be even more sensitive to heat than those from shoal waters.

The temperature of most of the deep-sea samples ranged from 5° to 10°C when hauled aboard the Galathea, having warmed up from about 3°C while being brought to the surface. The air temperature in the tropics, like that of the surface water, ranged from 28° to 30°C. Room temperature in the Galathea laboratory was usually a few degrees higher, and the temperature in the stateroom used as a microbiological laboratory often exceeded 40°C. Consequently we were working near or beyond the threshold of temperature tolerance of many marine microbes.

In spite of haste in handling materials and precautionary measures designed to keep them cool, many of the more sensitive organisms were probably killed by the heat. Lacking a cold room in which to make the necessary transfers involving minute amounts of inocula (often only 0.01 ml), part of the material got warmed up to near laboratory temperature during the measuring, transfer, dilution, and inoculation of the bacteria therein. Fortunately, a good many of the deep-sea bacteria did survive the extreme change in climate to which they were subjected during sampling and analytical operations, but we do not know how many may have perished. Data summarized in Table I illustrate the loss of viability of bacteria in deep-sea samples intentionally subjected to different temperatures for 10 minutes prior to plating on nutrient agar.

Only a small percentage (2.3 to 4.7) of the bacteria survived heating to 50°C for 10 minutes and less than 20 per cent survived for 10 minutes at 40°C. Most of those that survived proved to be spore formers. From the data in Table I, it might appear that most of the deep-sea bacteria tolerated a temperature of 30°C for 10 minutes, but this may not be true because, even at "room" temperature, the samples were subjected for several seconds to temperatures between 30° and 40°C or higher. Perhaps all of

Table I. Relative numbers of bacteria in sediment samples from Philippine Trench which developed on nutrient agar after small portion of sample was held for 10 minutes at stated temperature. The results are expressed as percentages of the number of colonies which developed from portions of the same samples subjected to "room" temperature during rapid routine manipulations.

Station Number	Water depth	Rapid room	Held 10 minutes at		
			30° C	40° C	50° C
	meters	per cent	per cent	per cent	per cent
413	10 060	100	91.6	18.0	4.7
418	10 190	100	82.5	7.4	2.3
419	10 210	100	93.7	11.8	3.0
420	10 160	100	78.4	6.5	2.8

the more heat-sensitive microbes were lost. This should stress the importance of providing properly air-conditioned rooms for microbiological manipulations on subsequent deep-sea expeditions. Maintaining the organisms at *in situ* temperatures and pressures during their transposition from the deep-sea floor to the surface may also be a useful innovation.

Effect of Hydrostatic Pressure on Marine Microbes.

Although bacteria appear to require for growth or reproduction a hydrostatic pressure which is near that of their native environment, it seems likely that few if any are killed by the decompression resulting from their transposition from the deep-sea floor to the surface. Such decompression may actually be advantageous to the organisms, because the resultant adiabatic cooling (about 1.6°C from a depth of 10 000 meters to the surface) helps counteract warming during transposition through warmer surface water. Of course, microbes may be killed mechanically by the sudden release of pressure in a system supersaturated with gas, but in spite of the pressure, there is no more gas dissolved in deep-sea water than in surface water.

Prolonged storage of deep-sea sediment samples at refrigeration temperatures has resulted in the gradual death of the bacteria at atmospheric pressure. Very few living bacteria could be detected in sediment samples from the Philippine Trench (depth 10 000 meters) following six weeks' storage at 3° to 5°C at atmospheric pressure, although large numbers of barophilic bacteria have persisted for 30 months in similar samples maintained in the refrigerator at 1000 atm. Whether this die-off is directly attributable to reduced pressure or is an indirect effect on the metabolism and nutrition of the bacteria under the experimental conditions can be determined only by further investigations.

Working with freshly collected deep-sea material (less than an hour after it was hauled aboard the Galathea), we found many more bacteria developing in nutrient media incubated at *in situ* pressures than at atmospheric pressure. The barophilic property of deep-sea bacteria is illustrated by representative results with samples taken from the Philippine Trench (Table II).

Table II. Most probable numbers (MPN) of bacteria per gram wet weight demonstrated in sediment samples from the Philippine Trench by the minimum dilution method in nutrient medium incubated in refrigerator at different pressures.

Station Number	Location of station		Water depth	Incubation pressure	
	Latitude	Longitude		1 atm.	1000 atm.
	North	East	meters	MPN	MPN
413	10° 20′	126° 36′	10 060	2 300	760 000
418	10° 13′	126° 43′	10 190	930	3 500 000
419	10° 19′	126° 39′	10 210	680	210 000
420	10° 24′	126° 40′	10 160	8 400	920 000
421	10° 29′	126° 05′	1 000	540 000	0
422	10° 49′	126° 01′	1 960	2 300 000	0
424	10° 28′	126° 39′	10 120	5 900	2 800 000

The most probable numbers of bacteria were estimated by "Standard Methods for the Examination of Water and Sewage" (American Public Health Assoc., 1936), as amplified by Halvorsen and Ziegler (1933) and by Prescott *et al.* (1947). Methods of inoculating the nutrient medium and of applying pressure are outlined below.

From the data in Table II, it will be observed that from 10 to 100 times as many bacteria from a depth of about 10 000 meters grew in nutrient medium incubated at 1000 atm as the number which grew at 1 atm. We now know that the effect of hydrostatic pressure on bacteria is partly a function of the composition of the medium, suggesting that with proper nutrients there may be as many bacteria from the deep sea that would grow at 1 atm as at 1000 atm, but we have not yet learned what these proper nutrients might be.

Although data like those summarized in Table II indicate the existence of strict barophiles (high pressure dependent bacteria), as this progress report is written we must admit that the pressure picture appears to be somewhat more complicated. Be this as it may, finding more bacteria in deep-sea sediments growing at *in situ* pressures (1000 atm) than at 1 atm is regarded as conclusive evidence that most, if not all, of the bacteria were indigenous to the deep and that they are physiologically active at high pressures. This conclusion is supported by finding in nearby shallow sediments from the sides of the Philippine Trench large numbers of bacteria which grew at 1 atm and none which grew at 1000 atm. This latter observation agrees with the findings of ZoBell and Johnson (1949) and ZoBell and Oppenheimer (1950), who reported that surface-dwelling microbes fail to grow at deep-sea pressures and many are slowly killed in nutrient media when held at pressures ranging from 400 to 600 atm. According to Oppenheimer and ZoBell (1952), pressures ranging from 200 to 600 atm inhibited the normal growth of nearly all of 63 different species of marine bacteria, mostly from shoal water habitats. Five of these were killed in four days by compression to 200 atm, 11 were killed at 400 atm, and 23 were killed in four days at 600 atm.

Nutrient Media and Enumeration Procedures.

The nutrient medium employed routinely for demonstrating the most probable number of bacteria by the minimum dilution method had the following composition:

Peptone (Difco)	5.0 gm
Ferric phosphate	0.1 gm
Potassium nitrate	1.0 gm
Soluble starch	2.0 gm
Yeast extract (Difco)	1.0 gm
Sea Water	1000.0 ml

Following autoclave sterilization its pH was 7.7. It was dispensed in 9.0-ml quantities in 15-ml screw-cap bottles.

Into the first bottle of sterile medium in each series was introduced aseptically 1.0 gm of the sample. After vigorously shaking to distribute the sediment (or water) sample evenly throughout the medium, a 1.0-ml aliquot was transferred, with a semi-automatic pipette, to the second bottle of sterile medium. This gave a 1:10 dilution or provided a 0.1-gm inoculum. After similarly shaking this second bottle, 1.0 ml was removed to inoculate the third bottle of sterile medium to give a 1:100 dilution or a 0.01-gm inoculum. The dilution procedure was repeated seriatim by powers of 10 until the original sample was diluted to 1:1 000 000.

Assuming a random distribution of the bacteria in the sediment sample and throughout the dilution series, it follows that bacterial growth in the 1:10 000 and all lower dilutions but no growth in the 1:100 000 dilution, for example, would indicate the presence of at least 10 000 viable bacteria per gram of sample but not 100 000 per gram. The most probable number (MPN) of bacteria in certain samples was determined with greater accuracy by preparing quintuplets of each series. For example, finding growth in all 5 tubes of medium inoculated with the 1:10 series, 3 positive in the 1:100 series, and none of the 5 positive in the 1:1000 series would indicate a bacterial population (MPN) of 79 per gram.

For incubation at atmospheric pressure, the diluted material in the nutrient medium was left in the screw-cap bottles. These bottles provided about 5 ml of air space for aerobes. To estimate the abundance of anaerobic bacteria in the sediment samples, the inoculated bottles were filled to capacity with O_2-free medium and the caps screwed tightly in place to exclude atmospheric oxygen. Following incubation at the desired temperature and pressure, the medium was examined for evidence of bacterial growth as manifested by increased turbidity of the medium or by finding large numbers of bacteria by direct microscopic examinations.

Ammonia liberation from peptone by ammonifiers:

$$R\text{-}NH_2 + HOH \rightarrow R\text{-}OH + NH_3$$

was detected by nesslerizing 0.2 ml of medium in a spot plate.

The presence of nitrate-reducing bacteria was indicated by the appearance of nitrite or by the disappearance of nitrate in the inoculated nutrient medium. Iodine was added to aliquots placed in a spot plate to test for the terminal presence of starch; its absence indicated the activity of starch-hydrolyzing bacteria. Sulfate-reducing bacteria were demonstrated in medium M-10-E:

Calcium lactate	3.5 gm
Magnesium sulfate, hydrated	0.2 gm
Potassium phosphate, dibasic	0.2 gm
Sodium sulfite	0.1 gm
Ferrous ammonium sulfate	0.1 gm
Ascorbic acid	0.1 gm
Peptone (Difco)	1.0 gm
Yeast extract (Difco)	1.0 gm
Bacto-agar (Difco)	3.0 gm
Sea water	1000.0 ml

It was adjusted to pH 7.5 following autoclave sterilization. The medium was dispensed in 15-ml screw-cap bottles, which were filled to capacity to displace all air, since the sulfate reducers are strict anaerobes. Following inoculation by serial dilutions and incubation, the presence of sulfate reducers was indicated by the blackening of the medium, resulting from the formation of ferrous sulfide:

$$SO_4^{--} + 10H \rightarrow H_2S + 4H_2O$$
$$H_2S + FeSO_4 \rightarrow FeS + H_2SO_4$$

Sea water enriched with 0.1 per cent ammonium phosphate (dibasic) and buffered with 0.2 per cent calcium carbonate was used to detect the presence of nitrifying bacteria. Following inoculation and incubation at the desired temperature and pressure, the enriched sea water was examined for the appearance of nitrite:

$$NH_4^+ + 2O_2 \rightarrow NO_2^- + 2H_2O$$

Nitrifiers which oxidize ammonium to nitrite were demonstrated in deep-sea sediment samples only when the inoculated medium was incubated at high pressures.

Inoculated media or samples to be held at high pressures were transferred to small glass vials, size 10 × 50 mm. After filling to capacity (5 ml) each vial was closed with a tapered No. 000 Neoprene stopper. When subjected to pressure in a steel vessel filled with hydraulic fluid, the stopper functioned as a piston, compressing the contents of the vial to approximately the same pressure as was built up in the steel vessel. Numerous tests have established that the compressed Neoprene piston stoppers provide an effective seal against contamination of any kind, the higher the pressure the better the seal.

High Pressure Apparatus.

The pressure cylinders (Figure 1) were constructed of 18-8 type 303 stainless steel. Such a vessel having an inside diameter of 1-3/8 inches and an inside length of 11 inches holds 25 10 × 50-mm stoppered culture tubes and weighs only 6 kg. The vessels were fabricated by drilling a radially central hole, with tapered bottom, in 12-inch lengths of 2-1/4-inch steel bar stock. The caps were prepared by machining 3-inch lengths of 3-inch steel bar stock as illustrated. Machining also provided for a male-threaded top extension for the permanent attachment of a needle valve and a perforated cone-shaped ceiling for exhausting air from the vessel. When fitted with an "O" ring and the vessel is filled level full with hydraulic fluid, the latter is displaced through the cap and attached needle valve when the cap is screwed on the cylinder.

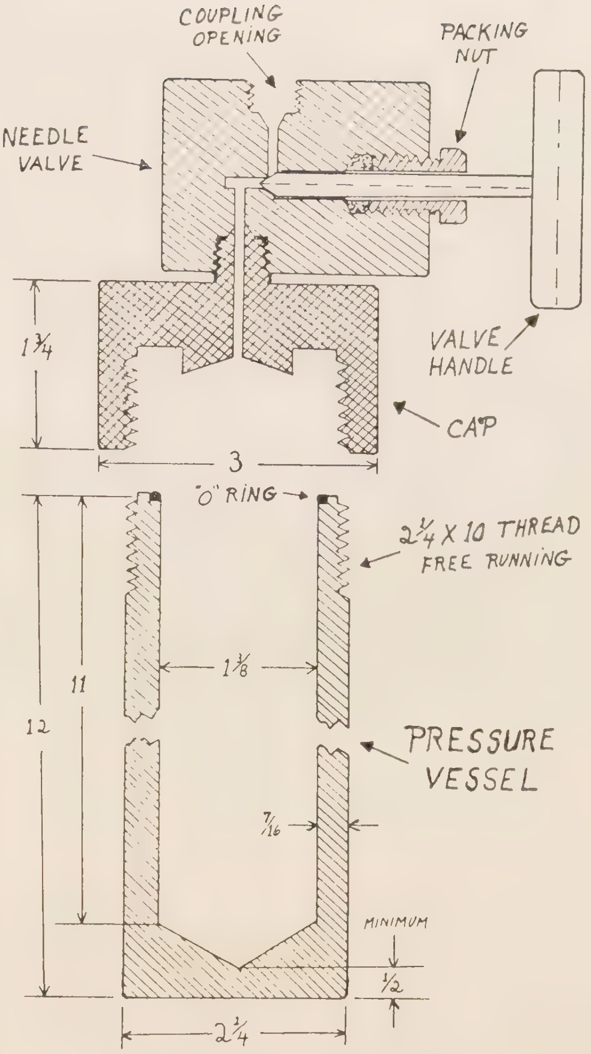

Fig. 1. Cross-section of stainless steel pressure vessel with its connecting cap and needle valve used for maintaining deep-sea sediment samples and bacterial cultures at high hydrostatic pressures. Dimensions are given in inches.

In practice the pressure vessel, equilibrated to the exact temperature at which it is to be incubated, is loaded with piston-stoppered culture tubes and filled level full with water at the same temperature. Hastily the cap is screwed on, an operation that can be performed by hand in a few seconds without the use of a wrench, and connected to the hydraulic pump (Figure 2). A few strokes with the handle of the pump produce a pressure up to 1000 atm in 20 to 30 seconds. After closing the needle valve, the pressurized vessel is disengaged from the pump for storage in the refrigerator or other thermostat. Con-

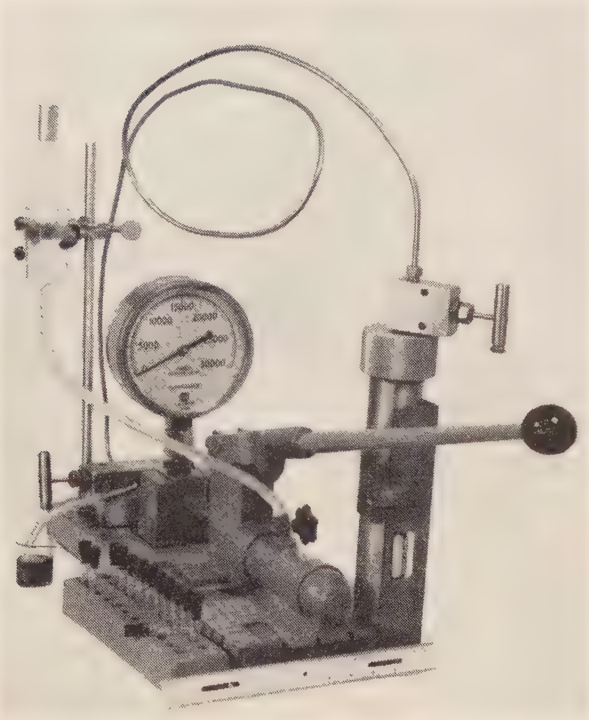

Fig. 2. High pressure vessel connected by semi-flexible steel tubing to hydraulic pump and Bourdon gauge. A rack of small culture tubes with piston stoppers is shown in foreground. ($^1/_{10}$ natural size).

stant pressure is maintained almost indefinitely provided the temperature is kept constant. The pressure changes between 6 and 7 atm per 1 °C change in temperature. Adiabatic heating amounts to about 2°C during compression to 1000 atm and it requires about 30 minutes for temperature equilibrium to be established by heat conduction in the thermostat, the half-life of the adiabatic temperature increase being between 5 and 10 minutes.

The portable pump pictured in Figure 2 was prepared from a hydraulic truck jack having a capacity of 30 tons or about 4000 atm. The pump is mounted on a block of wood along with the pressure gauge, high-pressure valves, hydraulic fluid reservoir, and semi-flexible steel tubing for connecting the pump to pressure vessel. The clamp on the corner of the assembly is for holding the pressure vessel in an upright position during pressurization. Immediately after applying pressure the needle valve on the pressure vessel is closed and the vessel is returned to the thermostat after disconnecting the top coupling.

The pumps were obtained from the Blackhawk Mfg. Co., Milwaukee, Wisconsin. Needles valves, steel tubing, couplings, and pressure gauges were supplied by the American Instrument Co., Silver Springs, Maryland. "O" rings were provided by The Parker Appliance Co., Cleveland, Ohio. The pressure vessels were prepared by the Special Developments Division, Scripps Institution of Oceanography, La Jolla, under the supervision of James M. Snodgrass. The hydraulic fluid employed in the pump was a 1:1 mixture of water and glycerol.

The pressure had to be released from the vessels before the latter could be opened for the examination of cultures or stored samples. For depressurization the vessel was reconnected to the pump and gauge assembly. Then pressure was applied by operating the pump until the pressure registered on the Bourdon gauge corresponded with the pressure initially applied to the vessel. If the pressure indicator did not move upon opening the needle valve, it showed that the pressure in the vessel was the same as that initially applied. Should the terminal pressure in the vessel be either more or less than that initially applied, the gauge would register an increase or decrease as the case might be. This procedure was always used to check the terminal pressures in the vessels. Interestingly, in thousands of cases the terminal pressure was always found to be the same as that initially applied, provided the temperature had been kept constant.

Air Express Shipment of Pressurized Samples.

Most of the microbiological analyses were made on the Galathea. However, because of their great significance, several sub-samples of sediment from the Philippine Trench were shipped by air express from Cebu to California, where they were examined in our laboratories at the Scripps Institution of Oceanography. This unique operation was made possible only through the cooperation of personnel from several organizations, including the officers and men on the Galathea, the East Asiatic Company, Royal Danish Consulate Service, Philippine Airlines, and the University of California.

Indispensable services were rendered by Mr. KJELD DANOE, who had our high pressure (1000 atm) vessels, containing sediment samples recently taken from the bottom of the Philippine Trench, insulated and packed in dry ice at Cebu for sending by air express to Manila. There this unique package was received two hours later by GUSTAV HALBERG and K. RAASCHOU NIELSEN, who made arrangements for its immediate transfer to a refrigerator on a Philippine Airlines plane. Thirty hours later the P.A.L. hostess placed the refrigerated pressurized vessel in the hands of a colleague, who met the plane in San Francisco, thanks to Royal Danish Navy radiograms that had forwarded instructions from the Galathea. Neither the temperature nor the pressure of the vessels changed perceptibly from the time they left the Galathea until they were in the laboratory at La Jolla. Examination by direct microscopic and cultural procedures confirmed the presence of numerous living bacteria in sediment samples from depths exceeding 10 000 meters.

Direct Microscopic Observations.

As soon as time permitted on the Galathea, small sub-samples of deep-sea sediment were examined with a phase contrast microscope at a magnification of 970 diameters. By means of a sterile platinum loop designed to deliver approximately 0.01 ml, portions were spread evenly over an area of 1.0 cm^2 on a clean glass slide and protected with a cover glass. Each bacterium observed in the area (0.0002 cm^2) covered by one field of the microscope represents 500 bacteria per 0.01 ml or 50 000 per ml of the original sample. With samples containing fewer than 50 000 per ml, it was necessary to scan several fields in order to find any bacteria. It so happened, however, that a good many of the sediment samples had bacterial populations exceeding 10^5 per ml. Thus, in spite of the obscuring effects of sediment particles with which the bacteria were associated, several bacteria were observed in some fields.

The first significant microscopic observation was made on a sample of silty clay dredged from a depth of 8870 meters in the Philippine Trench on 13 July 1951 at Station No. 412. Twelve sub-samples were prepared for microscopic examination; 50 or more fields of each being scanned. In nearly every field were found definite discrete bacterial cells, including ten different morphological types. Most common were non-sporulating rods with rounded ends, size about 0.5 microns in width by from 2 to 3 microns in length. Fairly abundant were capsulated ovoid rods having an average width of 0.8 microns and a length of 2 microns. Slender rods, 0.6 microns in width and up to 6 microns in length were found attached to sediment particles. Also recognized were several small vibrio, two different types of sporulating bacilli, two kinds of spirilla, and a few diplococci. Motility was not observed in wet preparations. Ostensibly the deep-sea bacteria lose their powers of locomotion due to the change in climate (lower pressure and higher temperature), because it was established by subsequent observations that the vibrio and some of the rods are flagellated.

These microscopic observations on the sediment sample from Galathea Station No. 412 were considered as presumptive evidence for the occurrence of bacteria from a depth of 8870 meters. However, conclusive evidence that they were indigenous species in this, and, eventually, in sediment samples from even greater depths had to await cultural tests, the first of which were completed 24 July 1951. Also observed in this sediment sample were a few empty diatom tests and some fish scales with attached bacteria. There was no evidence of cellulose fibers or of any kind of particulate organic matter besides bacterial cells. The absence of plankton organisms helped to rule out the possibility of the bacteria's having been picked up inadvertently while the dredge was passing through the photosynthetic zone, where the bacterial population was of the order of 10^3/ml.

The microscope also revealed the presence of bacteria in the topmost strata of a clay core collected 15 July 1951 at Station No. 413 from a depth of 10 060 meters. The core was 75 cm long. Detecting no bacteria in the lower strata of the core either by cultural or by direct microscopic examination is highly significant; negative results proved that sediment samples could be collected and analyzed on the Galathea without contamination. The topmost 0.1 cm layer of sediment was estimated to contain at least 3×10^7 bacteria per ml. Cultural methods showed the presence of 7.6×10^5 bacteria which grew at 1000 atm and only 2.3×10^3 which grew at 1 atm.

Predominating in the clay sample from Station No. 413 were rod-shaped bacteria with only a few helicoidal-shaped (vibrio and spirilla) cells, and still fewer spherical-shaped (cocci) bacteria. A good many of the bacteria occured in pairs or short chains, suggesting that the bacteria were reproducing. No protozoans, or other form of microscopic life other than bacteria, were observed.

It was extremely difficult to distinguish bacteria from sediment particles in clay samples dredged from depths of 10 190 and 10 210 meters at Stations No. 418 and 419 respectively. The direct microscopic examination of material dissected from the interior of balls of clay revealed the presence of fewer than 10^5 bacteria per ml, but exterior material was primarily from the mud-water interface. None of the bacteria observed in wet preparations exhibited any motility. Most of the bacteria were small, 1 to 2 microns long by 0.5 to 0.8 microns in diameter.

That the majority of them came from the deep-sea floor was indicated by cultural tests; the MPN at 1000 atm being 10^5 to 10^6 per ml as compared with MPN of only 10^2 per ml at 1 atm (see Table II).

The microscopic examination of greyish-green clay from a depth of 10 120 meters at Station No. 424 was more rewarding. Besides showing the presence of numerous bacilli (order of 10^7 per ml) there were many large (1.6×8 microns) spirilla unlike any bacteria previously described. None of the latter appeared among the many bacteria that grew in nutrient media incubated at 1000 atm (MPN $2.8 < 10^6$ per ml). The microscope also showed many bodies believed to be fungous spores. None of these germinated in nutrient medium incubated at 1000 atm, but in similar medium incubated at 1 atm bacteria were overgrown by fungi. This observation suggests the occurrence of viable fungous spores on the deep-sea floor. Failure to find fungous mycelial material in any of the deep-sea samples indicates that fungi are not growing on the deep-sea floor. Four different kinds of diatom tests were observed with no evidence of protoplasm.

A good many of the minimum dilution cultures prepared for MPN determinations were examined microscopically to confirm bacterial growth. Most of the deep-sea bacteria were morphologically similar to those from soil and shallow water environments with which we are more familiar, showing even less variety among the forms found. Short rods predominated. About 5 per cent were vibrio. Cocci were encountered only occasionally. Differential staining procedures proved that the majority of the deep-sea bacteria are Gram-negative. Capsulated forms were common. Endospores were observed in about 20 per cent of the bacilli.

Physiological Characteristics of Bacteria From Philippine Trench.

The deep-sea bacteria exhibited considerable physiological versatility in differential media at 1000 atm (Table III). Apparently there were almost as many anaerobes as aerobes and a good many reduced nitrate. Some seemed to be able grow in the absence of free oxygen by utilizing nitrate as the hydrogen acceptor. The sulfate reducers were the only obligate anaerobes demonstrated.

The deep-sea nitrifiers differ in their activity at high pressure from surface-dwelling forms as do the nitrate reducers. Nitrate reduction by several shoal water species, which have been tested by ZoBell and Budge (1954), is retarded by pressures of 400 to 600 atm and at 1000 atm their nitratase system is slowly inactivated.

Table III. Minimum numbers of different physiological types of bacteria detected per ml of sediment from the Philippine Trench.

Station number Water depth in meters	418 10 190	419 10 210	420 10 160	424 10 120
Total aerobic bacteria	10^6	10^5	10^5	10^6
Total anaerobic bacteria	10^5	10^5	10^5	10^5
Starch hydrolyzers	10^3	10^2	10^2	10^3
Nitrate reducers	10^5	10^4	10^5	10^5
Sulfate reducers	10^2	10	10^2	0
Ammonifiers	10^5	10^4	10^5	10^5
Nitrifiers	10	0	0	10

Bacteria in Indian Ocean Deeps.

Two sediment samples, suitable for bacteriological analyses, were obtained from depths exceeding 7000 meters in the Indian Ocean. Large numbers of viable bacteria were found in both samples, but surprisingly not nearly as many as in sediment samples taken from the Philippine Trench at depths exceeding 10 000 meters. Moreover, almost as many bacteria grew in nutrient medium at 1 atm as at 700 atm, and only a few from the Sunda and Weber Deeps grew at 1000 atm (Table IV).

Finding in these deeps starch hydrolyzers, nitrate reducers, sulfate reducers, ammonifiers, and nitrifiers which were active in differential media at 700 atm indicates that they are indigenous species which are probably active *in situ*. The activity of the deep-sea bacteria *in situ* is probably limited by the nutrient content of sea water and sediment and not by the high hydrostatic pressure or low temperature.

Bacteria in Kermadec-Tonga Trench.

Barophilic bacteria were found in 4 different sediment samples from the Kermadec-Tonga Trench (Table V).

Unlike the microflora found predominating in the Philippine Trench, nearly as many and in one sediment sample from the Kermadec-Tonga Trench (Station No. 686) more bacteria developed in nutrient media incubated at 1 atm than at high *(in situ)* pressures when isolates were examined. The inability of these bacteria recovered from the deep-sea floor to reproduce at *in situ* pressures suggests that

Table IV. Most probable numbers (MPN) of bacteria per gram wet weight demonstrated in sediment samples from Indian Ocean by minimum dilution method in nutrient media incubated in refrigerator at different pressures.

Station number	463 (Sunda Deep)	492 (Weber Deep)
Station location	10°16′ S × 109°51′ E	5°31′ S × 131°01′ E
Water depth	7020 meters	7250 meters
MPN at 1 atm	690 000	810 000
MPN at 700 atm	1 050 000	2 300 000
MPN at 1000 atm	4 800	17 000
Starch hydrolyzers at 700 atm	1 000	1 000
Nitrate reducers at 700 atm	10 000	10 000
Sulfate reducers at 700 atm	100	10
Ammonifiers at 700 atm	100 000	10 000
Nitrifiers at 700 atm	0	10

Table V. Minimum numbers of bacteria per gram of sediment from the Kermadec-Tonga Trench as determined by minimum dilution method in differential media incubated in refrigerator at different pressures.

Station number	649	650	658	686
Latitude	35°15′ S	32°20′ S	35°51′ S	28°30′ S
Longitude	178°40′ W	176°54′ W	178°31′ W	176°53′ W
Water depth (meters)	8300	6620	6720	9820
Total aerobes at 1 atm	10^5	10^6	10^4	10^6
Total aerobes at near *in situ* pressure*	10^6	10^6	10^6	10^5
Total anaerobes at 1 atm	10^4	10^6	10^5	
Starch hydrolyzers at 1 atm	0	10		
Nitrate reducers at 1 atm	0	0		
Sulfate reducers at 1 atm	0	0		

* Since the pressure-depth gradient in the sea approximates 0.1 atm/M, nutrient media inoculated with these four sediment samples were incubated at about 850, 680, 790. and 1000 atm respectively.

Table VI. Minimum numbers of bacteria per gram wet weight of sediment from different core depth detected in nutrient media incubated in refrigerator at 1 atm.

Station number	677		686	
Location of station	28°30′ S × 175°53′ W		20°53′ S × 173°31′ W	
Water depth	9190 meters		9820 meters	
Core depth	Aerobes	Anaerobes	Aerobes	Anaerobes
0-5 cm	1 000 000	1 000	1 000 000	1 000 000
5-10 cm	1 000 000	100 000	1 000 000	1 000 000
10-15 cm	100 000	10 000	1 000 000	100 000
15-20 cm	1 000 000	100 000	1 000 000	100 000
20-25 cm	100 000	10 000	1 000 000	10 000
25-30 cm	10 000	1 000	1 000 000	1 000
45-50 cm			10 000	10 000
85-90 cm			10 000	1 000

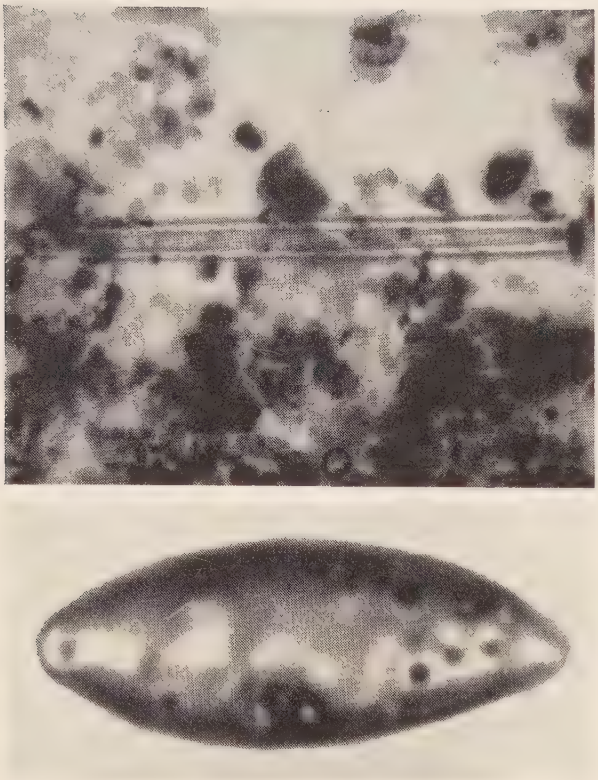

Fig. 3. Photomicrographs of two apparently intact diatoms found in deep-sea sediment following two years' storage in refrigerator at a pressure of 1000 atm.

they are not native to the deep-sea floor. The implication is that they have sunk to the sea floor where they may remain dormant for long periods of time. Such forms that tolerate high pressure without being able to reproduce are termed *baroduric*.

What appeared to be baroduric foraminifera and diatoms were detected in some of the Kermadec-Tonga Trench sediment samples examined by phase contrast microscope. This was confirmed by E. J. F. Wood (1956) working in our laboratory at La Jolla two years after the samples were taken. Since their collection the sediment samples had been stored in piston-stoppered tubes under conditions which were approximately isothermic and isobaric with the environment from which originally taken. Every one in the Scripps Institution laboratory who examined these preparations agreed that certain *Globigerina* contained protoplasm as did the *Coscinodiscus* and *Navicula* specimens. Extensive efforts to cultivate these foraminifera and diatoms have been unsuccessful. They are believed to be transient or adventitious forms which, like some of the baroduric bacteria, have sunk to the deep-sea floor. Regardless of their origin or significance, it is noteworthy that they have been preserved in refrigerated pressure vessels for many months. Two of the diatoms are shown in Figure 3.

The prolonged survival of baroduric bacteria buried at considerable depth was indicated by finding them in adundance to the bottom of cores collected from the Kermadec-Tonga Trench (Table VI). The vertical distribution of aerobes as well as anaerobes appeared to be sporadic, the general trend being decreasing abundance with core depth. Finding numerous aerobes buried at depths where there is probably no free oxygen constitutes further evidence of their dormancy. Some activity of bacteria is indicated by changes with core depth in the non-conservative chemical content of the sediment.

Chemical Content of Deep-Sea Cores.

Portions of two cores from the Kermadec-Tonga Trench were preserved in sealed bottles and brought back to the Scripps Institution laboratory for chemical analysis. Water content was determined by subtracting the constant dry weight (at 105°C) from the initial wet weight. The dried sediment was used for determining organic carbon, carbonate, Kjeldahl nitrogen, ammonia nitrogen, and sulfate.

Organic carbon was estimated by oxidizing at boiling point with a mixture of concentrated sulfuric acid, potassium iodate, and C.P. oxygen after first liberating carbonate carbon by treatment with phosphoric acid and flushing with a stream of pure nitrogen. The carbon dioxide resulting from both treatments was collected (separately) in standard barium hydroxide solution which was back-titrated with N/100 hydrochloric acid. The method of Bien (1952) for determining carbonate and organic carbon was used. This method employs a closed system which eliminates erroneous results from atmospheric CO_2.

Ammonia was driven off weighed sediment samples by sodium hydroxide treatment. Micro-Kjeldahl procedures were employed for determining organic nitrogen. Weighed samples were washed several times with distilled water accompanied by mechanical agitation to leach out sulfate, which was then determined gravimetrically as its barium salt. Results of the chemical analyses are summarized in Table VII.

The low carbonate content was expected, since carbonate in sediments usually decreases with depth in the ocean (Kuenen, 1950). This may be due to the increased solubility of calcium carbonate at the lower pH of sea water associated with the high hydrostatic pressure (Buch and Gripenberg, 1932).

Table VII. Certain non-conservative chemical constituents found in different strata of two mud cores from the Kermadec-Tonga Trench. Values are recored as milligrams per gram of dried (at 105°C) sediment.

Core from Galathea Station No. 677; water depth 9190 meters.

Core depth	Water content	Carbonate content	Organic carbon	Ammonia nitrogen	Kjeldahl nitrogen	Sulfate content
cm	per cent	mg/gm	mg/gm	mg/gm	mg/gm	mg/gm
0-5	46.2	0.7	0.5	0.8	0.5	1.9
5-10	43.8	0.0	0.2	0.2	0.3	1.5
10-15	40.1	0.2	0.1	0.1	0.3	1.2
15-20	40.0	0.6	0.2	0.1	0.3	1.6
20-25	41.8	0.2	0.2	0.1	0.4	1.2
25-28	38.4	0.4	0.1	0.1	0.3	0.9

Core from Galathea Station No. 686; water depth 9820 meters.

Core depth	Water content	Carbonate content	Organic carbon	Ammonia nitrogen	Kjeldahl nitrogen	Sulfate content
cm	per cent	mg/gm	mg/gm	mg/gm	mg/gm	mg/gm
0-10	53.7	0.2	0.3	0.1	0.2	2.0
15-20	51.7	0.5	0.3	–	0.2	1.6
25-30	50.7	0.5	0.2	0.2	0.2	1.3
35-40	52.5	0.3	0.3	0.1	0.3	1.1
45-50	53.0	–	0.1	0.0	0.1	–
55-60	50.8	0.2	0.2	0.1	0.3	0.2
65-70	53.4	0.4	0.2	0.0	0.4	0.4
75-80	52.0	0.2	0.2	–	0.2	0.2
85-90	47.7	–	0.2	0.1	0.2	–

The organic carbon as well as the organic nitrogen content of the deep-sea sediments was very low; in the deeper core strata the C/N ratio was 1:1. Total contents and the C/N ratios are considerably lower than in near-shore sediments, conditions which have been noted by Wiseman and Bennett (1940) and by Arrhenius (1952). Arrhenius postulates that the low C/N ratios in deep-sea clay deposits may be caused by some property, e.g., low calcium carbonate content, of the clay favoring conservation of nitrogen during the low rate of organic matter deposition, or it might be a reflection of differences in the way in which organic matter is decomposed in the deep sea. Most likely the relatively abundant ammonia-nitrogen content of the deep-sea deposits has resulted from the decomposition of proteinaceous materials. Bacteria (ammonifiers) which liberate ammonium from proteinaceous material were detected in virtually all deep-sea sediments tested for their presence.

There seems to be a general trend of decreasing organic content with core depth, which suggests its slow oxidation. In the absence of any obvious supply of free oxygen below the mud-water interface, the organic matter must be attacked by anaerobes, if by any kind of bacteria. The rate of attack appears to be very slow. Sulfate-reducing bacteria could account for the slow oxidation of organic matter in strictly anaerobic environments. Sulfate-reducing bacteria have been found in deep-sea sediments and, interestingly, there is a definite decrease in the sulfate content of the deep-sea cores.

Barophilic Sulfate-Reducing Bacteria.

Because of their importance as geochemical agents, special effort was devoted to the detection of sulfate-reducing bacteria in deep-sea sediment samples collected by the Galathea. Besides reducing sulfate to sulfide and oxidizing a great variety of organic compounds, certain sulfate reducers fix nitrogen (Sisler and ZoBell, 1951), and utilize molecular hydrogen (ZoBell, 1947; Sisler and ZoBell, 1950). Sulfate-reducing bacteria, which commonly occur in near-shore sediments (ZoBell and Rittenberg, 1948), were also found by Morita (1954) in several ocean basins. Populations exceeding 100 per gram of wet sediment were demonstrated in collections from a depth of 5032 meters at Mid-Pacific Station No. 36 (MORITA and ZOBELL, 1955).

As shown in Table III above, barophilic sulfate-reducing bacteria were demonstrated in Philippine Trench sediment samples from depths exceeding 10 000 meters. Such bacteria which grew at 700 atm were also demonstrated in bottom deposits from the Sunda Deep and the Weber Deep (see Table IV). Sulfate reducers from the Weber Deep have been maintained in pressure vessels at 3-5°C and 700 atm for more than 4 years and are still under observation at the Scripps Institution. Upon decompressing and opening the pressure vessel for the examination of some of the original sediment sample, a strong odor of hydrogen sulfide emanated, indicating activity of the organisms during storage. Small quantities of the mud were used to inoculate medium M-10-E in piston-stoppered tubes for enrichment in the refrigerator at 700 atm. After 60 days' incubation there was no evidence of sulfate reduction, but after 10 months sulfide had been produced in all tubes of medium M-10-E inoculated with this stored mud from the Weber Deep (7250 meters). The uninoculated controls were negative. There was no evidence of sulfate reduction in similar medium after 17 months' incubation at 1 atm in medium inoculated either with some of the original mud sample or with enrichment cultures that developed at 700 atm.

The obligate barophilic sulfate-reducing bacteria from the Weber Deep have been transplanted four successive times and kept growing at 3-5°C and 700 atm. With the cooperation of Dr. JAMES W. BARTHOLOMEW, electron micrographs were made. They show a small ovoid-shaped microbe about 0.3 microns in width by 0.5 to 0.8 microns in length, which differs in both shape and size from other known sulfate reducers commonly classified as *Desulfovibrio* species. Though highly pleomorphic, known *Desulfovibrio* species are usually comma-shaped organisms 0.5 to 1.0 by 3 to 5 microns in size. The barophilic sulfate reducer from the Weber Deep is believed to be a new genus, but further studies must precede its naming. Like most barophilic bacteria, it grows very slowly (ZOBELL and MORITA, 1957).

An Enigma in Bacterial Taxonomy.

In their unique ability to grow at high hydrostatic pressures, a good many of the bacteria isolated from the deep sea differ from known or described species whose habitat is soil, sewage, near-shore sediments, and other surface or shallow-water environments. However, pressure tolerance is probably not a sufficiently distinctive characteristic to delineate species, particularly since the deep-sea bacteria may have become acclimatized to high pressure while sinking from the surface, or their pressure tolerance may be associated with the composition of the medium.

Ordinarily, the taxonomic position of bacteria is based upon their physiological, cultural, and morphological characteristics as determined at 1 atm. Since some of these characteristics are altered and others are indeterminate at high pressure, we are confronted by an enigma in bacterial taxonomy. At least superficially a good many of the deep-sea bacteria appear to be new species or even new genera, but this can be established only by much more study.

The only deep-sea microbe to which we have applied a generic name is a small (0.4 micron) Gram-negative sphere, usually occurring singly but occasionally in pairs. It has exhibited no evidence of motility and does not form endospores. It liquefies gelatin and liberates ammonia from peptone in sea water medium in the refrigerator at 1000 atm. It oxidizes glucose with the formation of acid; sucrose, lactose, and starch are not attacked. In the refrigerator (3-5°C) it survives at 1 atm, but is killed in a few minutes when warmed to 25°C. It was isolated from two different mud samples from the Philippine Trench. Tentatively it has been named *Bathycoccus galathea*. The Greek suffix *bathy-* denotes great depth and *coccus* indicates that the cells are spherical.

Oceanographic Significance of Deep-Sea Bacteria.

What is the ecological and oceanographic significance of the bacterial populations found in oceanic deeps? Are they primarily passive inhabitants on the deep-sea floor or is their rate of metabolism and reproduction rapid enough for them to affect substantially chemical or biological conditions? Our observations prove only the presence of viable bacteria in some of the deepest parts of the ocean and show that these deep-sea bacteria are physiologically active in the laboratory under experimental conditions designed to duplicate deep-sea conditions, including high hydrostatic pressure and low temperature. Prerequisite to assessing the oceanographic significance of these deep-sea bacterial populations is much more information on the circulation of water masses, the amounts of organic matter reaching the deep-sea floor, the non-conservative chemical composition of the water and bottom deposits, abundance and growth rates of other organisms inhabiting the deeps, and more information on the characteristics of the bacteria.

An estimate of an average bacterial population of 10^6 per ml in the topmost cm of deep-sea sediment is believed to be conservatively low. Approximately this many were demonstrated in nutrient medium by the minimum dilution method, which does not detect all living microbes, since no one medium can provide for the nutrient requirements and essential environmental conditions for the growth of all bacteria. Moreover, groups of bacteria occurring in agglomerates or attached to solid particles register only as single individuals in the minimum dilution method. Extensive experience by bacteriologists who have been analyzing soil, sewage, milk, and similar materials for several decades shows that conventional cultural methods usually detect only about 10 per cent of the viable bacterial population. Actually bacterial populations of the order of 10^7 per ml of deep-sea sediment were indicated by the direct microscopic method, but the microscope fails to distinguish living from dead bacteria.

Taking 10^6 per ml as the order of magnitude of the bacterial population and considering these bacteria to contain an average of 2×10^{-13} gm of organic carbon per cell, it follows that 1.0 ml of such sediment would contain 2×10^{-7} gm of bacterial carbon, or 0.2 mg per liter. In a layer 1 cm thick there would be 2 mg of bacterial carbon per square meter.

Such a standing crop of bacteria may contribute substantially to the nutrition of benthic animals. Protozoans, worms, sponges, filter feeders, and mud eaters are among the animals known to ingest and digest bacteria (ZoBell and Feltham, 1938). Certain animals can survive and thrive on an exclusive diet of bacteria (ZoBell and Landon, 1937), and some can reduce the bacterial population of sea water to 10^2 to 10^3/ml. Bacteria consist largely of easily digestible proteins and lipids. Many are rich in vitamins and other accessory growth factors which may be beneficial to benthic fauna far removed from products of photosynthetic activity.

Kriss (1954) has stressed the importance of bacteria as food for marine animals and in the organic cycles in the sea. According to Kriss and Rukina (1952), the microbial biomass in marine sediments and overlying water column amounts to from 0.2 to 1.4 gm per square meter.

The extent to which bacteria contribute to the nutrition of deep-sea animals cannot be estimated from the standing crop or population of either, but must be based upon reproduction or growth rates. The population is only an expression of a dynamic balance between the rate of reproduction and the rate of death. Laboratory observations indicate that deep-sea bacteria reproduce (by transverse fission) once every 2 to 20 hours in nutrient medium incubated at 1000 atm and 3°C; somewhat slower in deep-sea sediment or sea water to which no nutrients have been added. They may be dormant *in situ,* as indeed many appear to be in the lower strata of cores from the Kermadec-Tonga Trench (Table VI), but at the mud-water interface they are probably reproducing. The low content of organic matter in deep-sea sediments and immediately overlying water must be attributable to bacterial activity, and there is pretty good evidence for the activity of sulfate-reducing bacteria. Should the rate of reproduction *in situ* be comparable to that found in the laboratory under conditions designed to simulate the *in situ* environment, we may think with confidence of an *in situ* reproduction rate which could provide a hundred or more bacterial "crops" per year, but other dynamic factors must be evaluated before concluding that this is a reasonable estimate.

The maximum amount of bacterial cell substance producible per unit of time is limited by the amount of available energy source. This is believed to consist largely of dissolved or colloidal organic matter reaching the bacteria. Chemosynthetic autotrophs may fix some carbon on the deep-sea floor, but such bacteria appear to play a very minor role. Of course, bacteria are highly efficient in recycling the organic waste products of animals, but there must be an influx of energy to keep the processes going. This energy, originating as fixed carbon in the photosynthetic zone, must reach the deep-sea floor primarily by settling or by the movements of water masses.

Ordinarily an average of one-third of the organic carbon assimilated by heterotrophic bacteria in dilute media is converted into bacterial cell substance, the other two-thirds being oxidized to CO_2. With similar efficiency a bacterial population of 10^6/ml representing a standing crop of 0.2 mg bacterial carbon per liter would require 0.6 mg organic carbon per liter and about the same amount of O_2. The complete oxidation of organic matter requires somewhat more than its own weight in O_2; 1.0 mg of various carbohydrates requiring 1.07 to 1.18 mg O_2, common fatty acids 1.06 to 2.97 mg O_2, triglycerides 2.40 to 2.92 mg O_2, amino acids and proteins 0.64 to 2.58 mg O_2/mg.

Replacing a bacterial population of 10^6/ml 100 times per year would require 60 mg of organic carbon per liter and somewhat more than this amount of O_2. This is much more than occurs in sea water at any one time, but throughout the year organic matter on the sea floor may be replenished by the movements of water masses and to a lesser extent by sedimentation; O_2 by diffusion and water movements. Apparently bacterial populations of the order of 10^6/ml occur only in the immediate vicinity of the mud-water interface, falling off rapidly with distance off the bottom. Only a few samples of sea water from depths exceeding 7000 meters and a meter or more off the bottom have been examined for the presence of bacteria, but all of these, like hundreds of water samples collected from depths exceeding 1000 meters, have bacterial populations of less than 10/ml. If this is representative of conditions throughout deep water masses, organic matter and O_2 from a water column of considerable thickness may be supplying the active biotic zone at the mud-water interface.

Besides oxidizing most kinds of organic matter with the consumption of O_2 and contributing to the nutrition of benthic fauna, bacteria may affect the non-conservative chemical composition of the deep-sea floor. The decomposition of organic matter probably results in the formation of complex marine humus and the liberation of phosphate, sulfate or sulfide, and nitrogenous compounds. Ammonifiers liberate ammonia from certain nitrogenous substances and nitrifiers may oxidize the ammonia to nitrite or nitrate. In the absence of free oxygen, sulfate reducers may produce hydrogen sulfide. If the latter diffuses into oxygenated waters, it may be oxidized with the formation of sulfate or sulfur. Though not detected on the Galathea Expedition, other bottom-dwelling bacteria may fix nitrogen or oxidize hydrogen or methane, which often result from the fermentation of organic compounds.

Bacteria in Water.

Although attention was concentrated on the microbial content of deep-sea sediments, several samples of sea water were examined for the presence of bacteria. Aseptic samples were collected in sterile evacuated bottles hermetically sealed with glass capillary tubes which could be sheared off at any desired depth to provide for the aspiration of water (ZoBell, 1941). Near-surface samples were collected in glass bottles tossed forward, with a hand line, off the bow of the Galathea in order to avoid contamination from the ship. Water samples from depths of 7000 to 8000 meters were collected in 300 ml collapsible rubber bulbs attached in properly spaced series to the hydrographic wire (Figure 4). At greater depths the elasticity of the rubber was adversely affected by the high pressure as has been described by ZoBell (1954).

From 12 July to 15 August 1951 a total of 44 surface water samples collected over the Philippine Trench were examined for bacteria by the minimum dilution method. In every one of these samples were detected from several hundred to a few thousand bacteria per ml, which grew in nutrient medium incubated at air temperature (ca. 30°C). There was no growth in similarly inoculated medium incubated at 1000 atm, and very little growth at 3-5°C, unlike the bacteria found in Philippine Trench sediments.

In organic-rich waters from Philippine Island bays and harbors visited by the Galathea were found

Table VIII. Minimum numbers of bacteria per ml of surface sea water collected on Galathea at different locations. The bacteria were demonstrated in nutrient medium incubated at air temperature and atmospheric pressure.

Total samples	General location of stations from which samples were collected	Date of collection	Bacteria per ml
2	Manila Bay	9-10 July	10^4 to 10^5
11	Over Philippine Trench	12-15 July	10^2 to 10^3
3	Tubajon Bay off Dinagat Island	17-19 July	10^3 to 10^4
12	Over Philippine Trench	21-24 July	10^2 to 10^3
2	Cebu Harbor	25 July	10^4 to 10^6
9	Over Philippine Trench	26-29 July	10^2 to 10^3
1	Kanlanuk Bay off Bucas Grande	30 July	10^4
2	Candos Bay off Lapinigan Island	31 July	10^4
8	Over Philippine Trench	2-8 August	10^2 to 10^3
6	Cebu Harbor	10-12 August	10^4 to 10^5
4	Over Philippine Trench	14-15 August	10^3

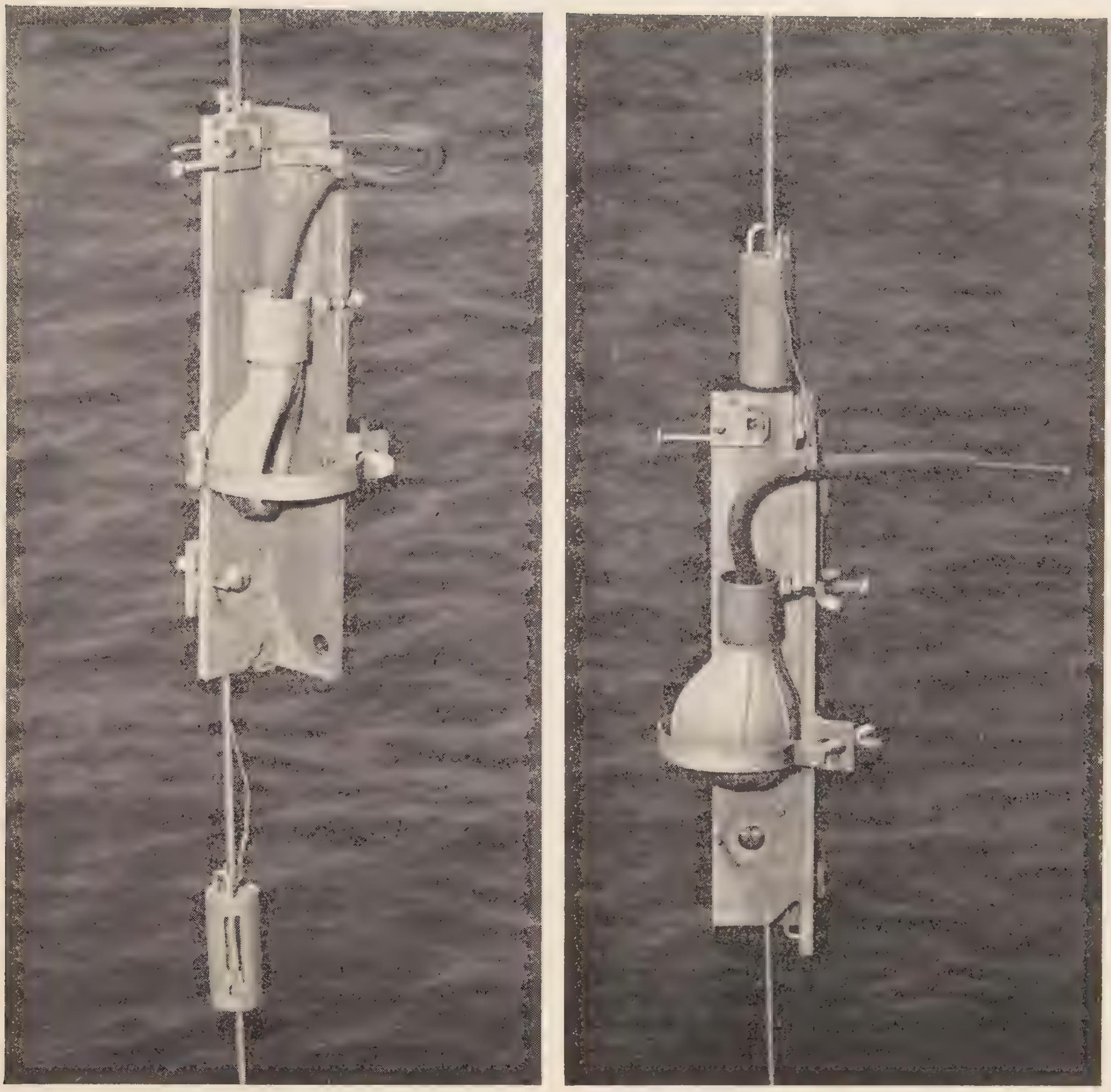

Fig. 4. Bacteriological sampler attached to hydrographic wire; at left the sterile rubber bulb is shown collapsed ready to be lowered into the water. Upon reaching the desired depth a messenger is dropped which shears off the capillary glass tubing thus permitting the thick-walled rubber tubing to flip out to the position shown at the right so water is aspirated from an area considerable distance from the apparatus in order to minimize self-contamination. Simultaneously the messenger suspended from the apparatus (left) is released, permitting it to drop for activating similar or other hydrographic apparatus at greater depth.

from 10 to 1000 times as many bacteria as in near-surface water collected over the Philippine Trench (Table VIII).

Throughout the photosynthetic zone over the Philippine Trench to a depth of 100 to 200 meters, the bacterial population ranged from 10^2 to 10^3 per ml. Not enough samples were analyzed to determine whether the vertical abundance of bacteria corresponded with vertical distribution of phytoplankton, as has been found to be the case in certain areas (ZoBell, 1946). At depths exceeding 1000 meters fewer than 10 bacteria per ml were found. In northern Pacific Ocean deeps Kriss (1952) found few bacteria in water samples, but in bottom sediments he found from 10^6 to 10^8 bacteria per gram.

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BATHYMETRIC FEATURES OF THE PHILIPPINE TRENCH

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INTRODUCTION

The Danish Deep Sea Expedition round the World in 1950-1952 worked in the deepest part of the Philippine Trench from July 12th to August 15th, 1951, interrupted only by four very short visits ashore. Although the principal object of the expedition was to investigate animal life on the bottom of the sea and in the deepest strata of water, it was necessary before each haul or sampling of the bottom to make a thorough examination of the topography of the seabed, not least because the actual bottom of a trench may be quite narrow and the jagged sides are absolutely destructive to the fishing gear. It was therefore necessary to crisscross the area to be examined, often for many hours, before the biological and hydrographical investigations could start, and in this manner an exceedingly great quantity of observations was collected, distributed over several hundred echo sections in all directions.

The manuscript was translated from the Danish by Mr P. Prom.

ECHO SOUNDINGS

The Echo Sounder

The echo sounder especially constructed for the "GALATHEA" was delivered by Kelvin-Hughes Ltd, of London, (MS-21, Type J & K with scale up to 9,000 m uncorrected). As the absorption of the sound waves in water increases with increasing oscillation, the frequency of 15 kc or upwards as used in most other ships would be inappropriate at these great depths, although high frequencies do give the best possibilities for a determination of the directions of the sound waves. The "GALATHEA"'s echo sounder was therefore designed for 10 kc, which combines good penetration through the water with an adequate determination of the direction of the beam.

The transmitter was of extra large type consisting of a 13,35 cm core of nickel rings in front of an air-filled reflector in a 58,40 cm tank (Fig. 1). It was located one-third of the length of the ship from the stem, about 2 m below the surface (draught of the ship 3 m), and the iron plating of the bottom was at this place replaced by a 6 mm thick, unpainted

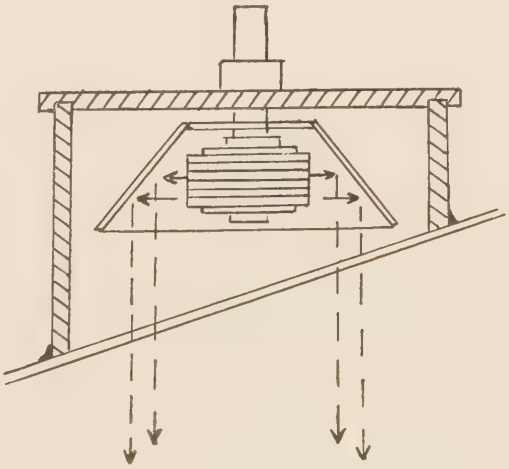


Fig. 1. Transmitter of echo sounder.

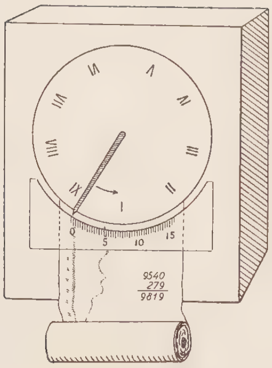


Fig. 2.
Recorder of echo sounder.

plate of stainless steel. The sound waves from the core of the transmitter are focused by the reflector into a beam which through the stainless steelplate passes vertically down into the water. Sounds of two different volumes may be transmitted, the minor volume combined with a short impulse, the major one with a long impulse. It appeared, however, that the minor volume was sufficient at all times and even to be preferred.

The receiver is exactly similar to the transmitter and located in the other side of the ship's bottom.

The echo received, and thus the depth, was recorded on the bridge by means of the apparatus shown in Fig. 2. As a rule the echo sounder was adjusted to transmit sound impulses 5 times a minute, and the recording arm would then rotate at a constant speed of 5 times a minute. By this adjustment the depth will be recorded on the paper sliding slowly past the scale by one mark every 12 seconds, which at a cruising speed of 8 knots corresponds to one recorded sounding for each 50 m. On passages between working areas a speed of 8 knots was frequently maintained, but during sounding operations the speed of the ship was generally lower, often only 3-4 knots.

When work was done in shallow water or it was desired to make a detailed examination of the bottom, the sounder was adjusted to 50 impulses per minute, but at that rate the scale, of course, ranges over only one-tenth of the usual depth interval.

At the 'normal' rate of transmission = 5 times a minute, the width of the paper corresponds to a depth of 1,500 m, but the transmission of sound may be moved ahead outside the paper, so that zero on the scale at the lefthand edge of the paper will correspond to the reception of echoes from depths of 1,000, 2,000, 3,000 m etc. up to 9,000 m, in which last case the adjustment will be equal to the first zero adjustment. When soundings are taken at adjustments 0-1,500 m and 9,000-10,500 m, the hand will at the instant of transmission make a small mark abreast of zero on the scale, but at high-power transmission the arm may, due to overshoot in the apparatus draw a short line extending to a depth of up to 200 m, and the recording of echoes from depths of 0-200 m and 9,000-9,200 m (uncorrected) may thus be more or less concealed by the next transmission mark. In case of the interval between 9,000 and 9,200 m this difficulty may, however, be overcome, if for every second transmission the adjustment is set in such a manner that the transmission mark will fall outside the paper and thereby be prevented from spoiling the reception of the echo of the preceding transmission. At depths of 0-200 m this difficulty may be obviated by the use of 50 transmissions per minute.

The recording of the hand on the paper is caused by an electric current which at the moment of reception will pass from the hand through the paper, which is constantly kept moist, to the base on which it rests, and as the paper is impregnated with sodium iodide a dot of free iodine will be deposited at each impulse. On a scale fastened to the apparatus the uncorrected depth may be read direct and noted at suitable intervals on the paper by means of an electric pencil. Supplementary readings during the subsequent compilation of the data may be made by means of a loose scale shortened in length corresponding to the normal contraction of the paper after drying. As, however, paper of different brands cannot be expected to contract equally, and as furthermore the amount of contraction will vary with the rate of drying, the original readings must always be regarded as the correct ones and subsequent readings be corrected accordingly. On board the "GALATHEA" the paper contracted somewhat more than had been calculated when the 'dry' scale was manufactured; so all subsequent readings have been corrected accordingly.

The principle of having the electric current release a dot of iodine possesses the great advantage that the rotating indicator arm will not have to make any movement to and from the paper at the moment of recording. The iodine deposited will, however, gradually evaporate so that the marks become weaker. If the paper is kept tightly rolled up on a central rod and stored in tight cases, the marks may, however, be kept fresh for several years. To be on the safe side, we did, however, immediately at the first cursory preparation of the observation data draw up all curves with a fine pencil line and at the same time photographed all important parts of the curves.

Accuracy of the Soundings

The “Galathea”’s echo sounder functioned to our full satisfaction. It was frequently inspected by the ship’s Chief Electrical Artificer and its rate of rotation was checked several times a day and adjusted as required. The apparatus was so designed that the rate of revolution might be so accurately adjusted as to give an error of maximum 0,2 ‰, and as the error in readings did not exceed 10 m, the total error of the uncorrected soundings might even at the greatest depth be kept at less than ± 30 m. To this must be added possible errors in the correction for deviations in the velocity of the sound due to changes in temperature, salinity and pressure at great depths. The apparatus was tuned to a speed of sound through the water of 1,500 m/sec. (820 fms./sec.), and the calculation of the correction mentioned was made according to D. J. Matthew’s tables, 2nd ed., 1939, but for the purpose of control we ourselves tried to calculate the correction on the basis of our own hydrographic observations in the Philippine Trench and found our calculations to be in close conformity with the values given in the tables. As in this area temperature and salinity vary but little with the seasons, the error in the correction can only be a small one, so the total error in the deepest soundings in the areas worked will be less than ± 45 m, and outside the working areas, when the rate of rotation was controlled less frequently, at most ± 75 m.

By way of comparison it may be stated that Maurer (1937) estimates the inaccuracy in the soundings taken by the “Emden” in the Philippine Trench in 1927 at ± 140 m, whereas van Huystee (1944) gives ± 100 m as the probable inaccuracy of the “Snellius”’ soundings in 1930, while according to Hess and Buell (1950) the inaccuracy of the “Cape Johnson”’s observations in 1945 is ± 91 m. The three research vessels here mentioned used low frequency tones and the echo was picked up by earphone and not as in the “Galathea” automatically recorded. When in October, 1951, the “Challenger” measured the great depths in the Marianas Deep – 10,863 m – an echo sounder of the same type as that of the “Galathea” was used, but nevertheless as far as the greatest depths were concerned an earphone was used, and by reckoning on a listening-in error of up to 37 m (Carruthers and Lawford, 1952), the total inaccuracy was fixed at ± 110 m (Wüst, 1952).

Spread of the Sound Beam

In most freighters and passengerships equipped with echo sounders for navigational purposes frequencies of 15-40 kc are used, and as it is practical to have the sounder register not only the vertical depths directly below the ship but also irregularities at some distance, it is so constructed that the apex of the conical beam transmitted has an angle of spread of up to 20° with the perpendicular. In survey work the beam should, however, be as narrow as possible, and the “Galathea”’s sounder was therefore designed to give a spread of only 8° with the perpendicular, or rather in such a way that the energy emitted which is greatest along the axis of the cone already at an angular distance of 8° from the axis decreases to such extent (up to 50 %) that echoes from more remote positions will not be registered.

In the course of our work, we learned, however, that so long as the ship was in relatively shallow waters the echo was returned from the entire base

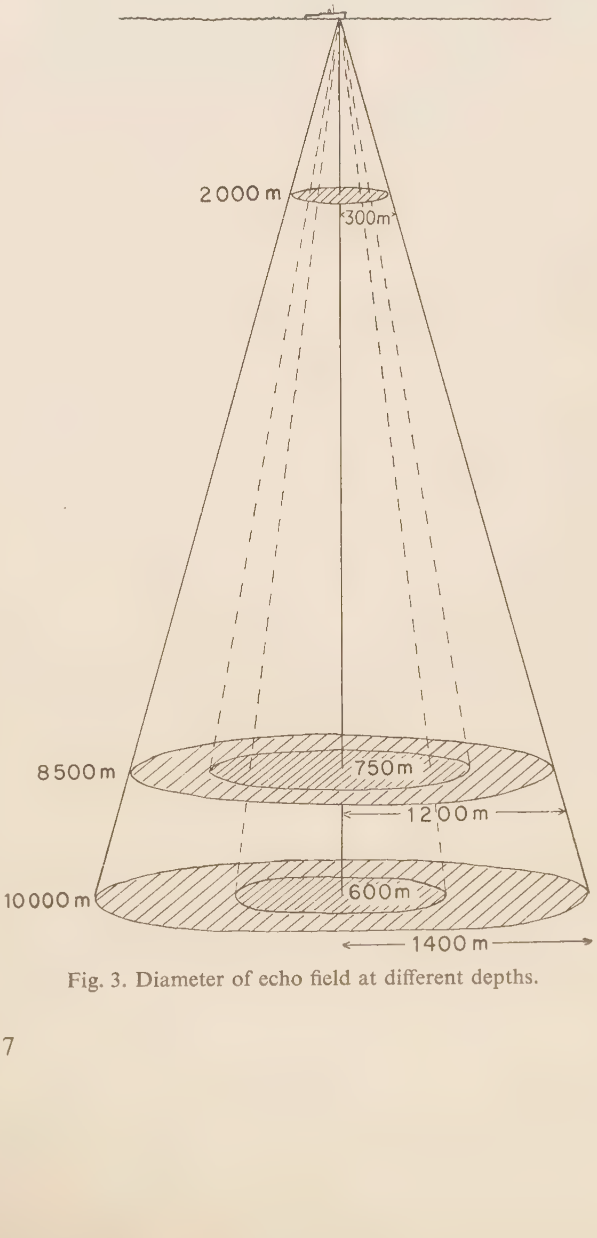


Fig. 3. Diameter of echo field at different depths.

on the bottom of this cone, so that at depths of, say, 2,000 m higher parts of the bottom out to about 600 m from the position of the ship were recorded. At greater depths, however, the part of the cone giving an echo was diminished until at a depth of 8,500 the apex angle was only 2 × 4.5° and at 10,000 m depth only 2 × 3.5° which corresponds to radii of the echo base of 750 m and 600 m, respectively. (Fig. 3). This is in close correspondence with the theoretical exposition by Hodgson and Fridriksson (1955) according to which the field that may be examined with an echo sounder is pear-shaped rather than conical.

The maximum spread can, however, be observed only under ideal reception conditions and when the echoing surfaces are of suitable size. Very frequently the echo will be received only with considerably less spread, mostly because the seabed is not sufficiently regular or because the horizontal surfaces are too small in extent.

A beam sea or swell may cause the ship to heel so much that a beam transmitted will strike the bottom at some distance from the side and at such an angle that the echo will not return to the receiver, or alternatively, a beam transmitted vertically towards the bottom may be thrown back just when the ship is heeling so much that the receiver will be unable to catch it. These problems were very much to the fore in the "DISCOVERY" in 1950 (Herdman, 1955), but we were only little troubled with these difficulties as the sea was calm during the greater part of our stay in the Philippine Trench and the "GALATHEA" was very stable in a seaway.

If the aim is to plot with the greatest possible exactitude the course of the depth curves particularly in the Philippine Trench where the deepest channel at places is exceedingly narrow, a spread of somewhat less than 600 m would be desirable. The spread is, however, not so great as to necessitate a calculation of the correction of the depths due to the greater distance from the circumference of the echo field. The difference between the vertical line to the centre of the field and the oblique line to the circumference will at depths of 10,000 m amount to only 0,2 %, or considerably less than the inaccuracy in measuring technique.

Echoes from Slopes

During the work of the expedition, in connection with hydrography as well as with sampling of the bottom or trawling, it happened quite frequently that at the beginning of the work we obtained a pure echo from the flat bottom of the deep channel at a depth of about 10,000 m, while during the next few hours another echo very gradually emerged from a level situated 100 or 150 m above the bottom without indication from intermediate depths (Fig. 4). This was due to the fact that during the work the ship was by the current carried in over the western side of the trench, where the bottom rises stepwise and very frequently has so steep slopes that they cannot return an echo to the ship, while at the same time two levels may come within the echo field (Fig. 5). If, on the other hand, the bottom rises without terraces but with a steep slope extending over so long a distance that the next horizontal level will not come within the echo field (Fig. 6) until the preceding level has disappeared, the registration of that level will gradually vanish, the marks spreading slightly beforehand. As this was often a characteristic of the eastern side of the trench, while the stepwise rise was more character-

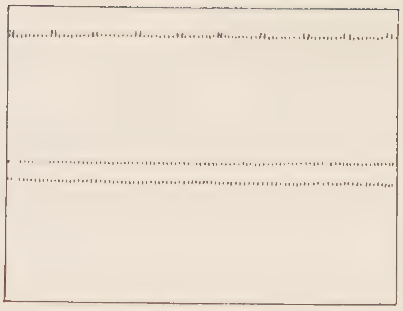


Fig. 4. Recording of echoes from two levels.

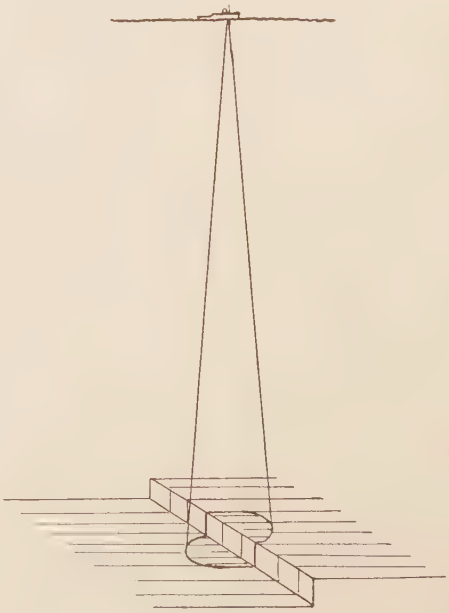


Fig. 5. Echo field distributed on two levels.

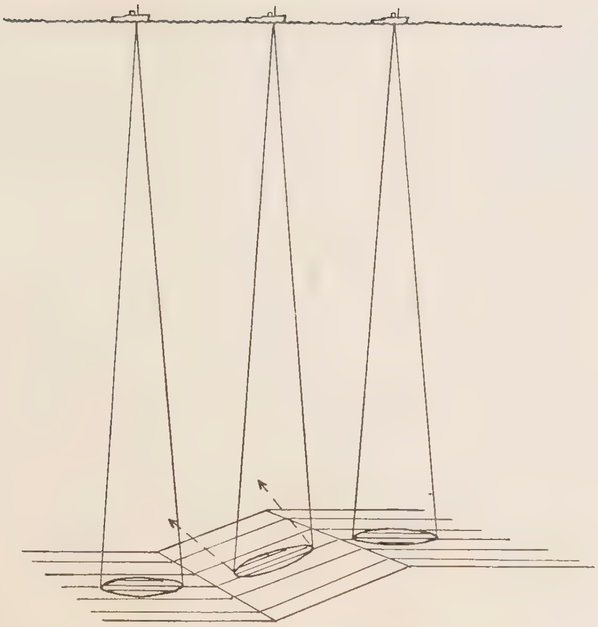


Fig. 6. The echo vanishes between the two horizontal levels.

istic of the western side, the spread of the sound beam was often an aid to us in keeping the ship in place over the middle of the trench during the 10-15 hours a series of operations might last.

A plane seabed need only slope very little in order to throw the echo so much to the side that it cannot be caught by the ship. In the course of our work we learned that as soon as the gradient exceeded 1 : 5 or 1 : 6 (about 10°) the echoes could not be recorded as one continuous curve – and as a rule not at all – even if all other conditions were ideal. In the U.S. Navy vessel "Cape Johnson", which during World War II was stationed in these waters, they frequently experienced this missing echo, just as we did. When, however, it is stated on the part of that ship that in such cases they had to make up to 10 sound transmissions before receiving an echo from certain areas of great depth, and they conclude from this fact that the seabed of the trench in such places must consist of too soft a material to reflect the sound, we must say, that according to our experiences the explanation must rather be that the ship for a time must have been over too steep a gradient of the bottom, and only received another echo when she again encountered a more horizontal bottom (Hess and Buell, 1950).

Air Bubbles in the Water

That air bubbles in the water in boisterous weather or if the ship is moving at high speed in a seaway will spoil the echo is a fact known in all ships, air being a substance which is particularly effective in reflecting sound. In this respect the "Galathea" may have been especially troubled due to her shallow draught, more particularly when both oil and freshwater tanks were almost empty after long stays at sea, and the ship was extra high in the water. Lacunae will therefore be found in our echograms from periods of bad weather and particularly in connection with the passage of two typhoons which even for a time compelled us to leave our working area.

ANALYSIS OF THE ECHOGRAMS FROM THE PHILIPPINE TRENCH

Echoes from two Levels

In the analysis of the echograms with a view to the preparation of a bathymetric chart of the Philippine Trench no difficulties are encountered so long as the sea bottom is horizontal and uniform so that only one echo curve will be drawn. When, however, the abovementioned declivities and slopes intervene, regard will have to be paid to the spread of the sound beam, as will appear from the following examples

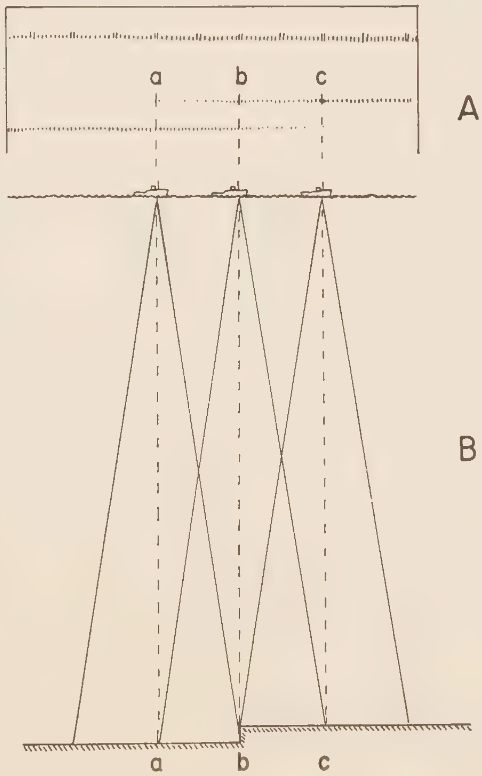


Fig. 7-A. Echogram showing a sharp transition from Level I to Level II of the seabed.
Fig. 7-B. Analysis of the echogram in Fig. 7-A.

in which the ship crossed the deep channel at right angles and constant speed.

The echogram in Fig. 7-A, which is to be read from left to right, shows that the echo from Level I begins to weaken from time a, while at the same position the higher level II manifests itself very slightly. At b the two curves are of equal power, corresponding to the fact that equal parts of the two levels are now within the area covered by the beam. Thereupon Level I disappears entirely at c, whereas Level II is registered at full force. The time marks on the paper and the speed of the ship show that the distance travelled between the positions a and c is 1,200 m over a depth of about 10,000 m, and the echogram must therefore be read in accordance with Fig. 7-B, in which, however, the angle of spread is highly exaggerated.

While the ship is in position a an echo of full power will be received from Level I, but Level II is just beginning to appear although it is still 600 m ahead. Having travelled 600 m (b) the ship must be right above the vertical slope and receives echoes of equal power from I and II, and only when she is 600 m in over the new level (c) the first level will disappear entirely from the recording.

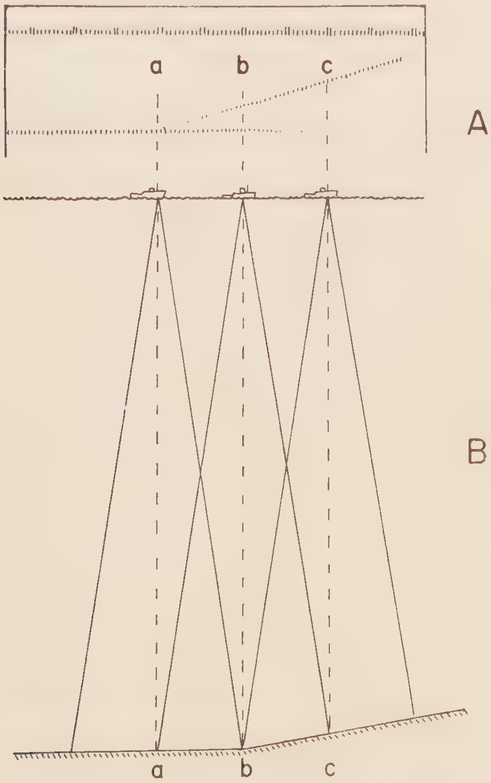


Fig. 8-A. Echogram showing transition from a horizontal level to a gently sloping level.
Fig. 8-B. Analysis of the echogram in Fig. 8-A.

Echo from a gradually sloping Seabed

In the example shown in Fig. 7 the declivity between the two levels is vertical, but in most cases the bottom will slope to some extent, and if the gradient does not exceed 1 : 5 we will have the situation shown in Fig. 8-A-B.

Just when the ship is 600 m from the place where the horizontal bottom (I) adjoins the sloping ground (II), the latter begins to show in the echogram (a) and, similarly Level I will only disappear entirely when the ship has got 600 m in over the sloping bottom. The strongest echo from Level II may not, however, be received from the place right below the ship but from a place a little farther ahead, but as already mentioned this is of very little importance in the measuring of the depths.

Examples of Echograms from the Philippine Trench

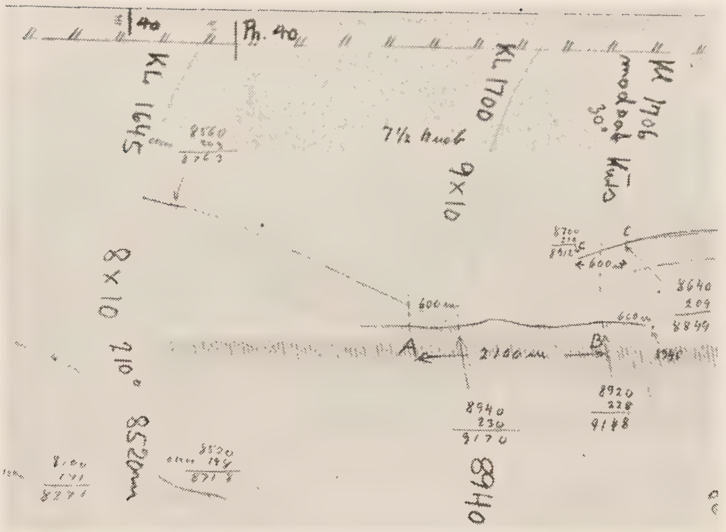
Even if these schematic echograms in actual fact will frequently be more or less distorted by irregularities in the sides of the trench, clear and unambiguous echograms have, however, in many cases been obtained during the many crossings of the deepest channel. An example, Section III in Plate I, is given in detail in Fig. 9-A-B.

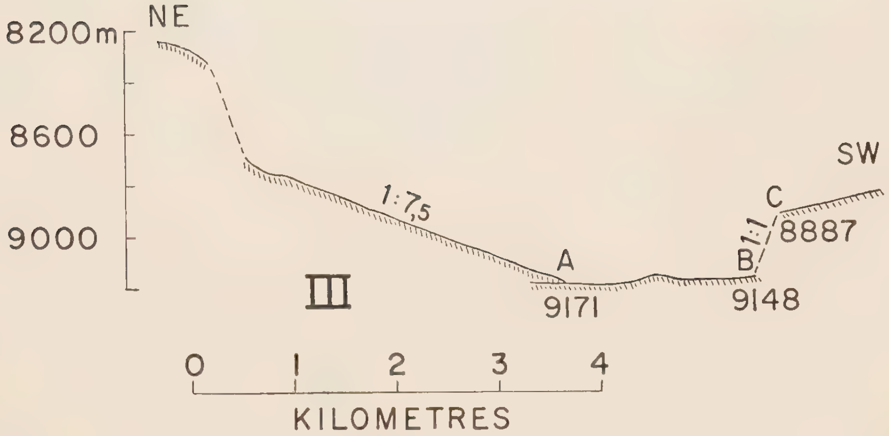
The middle of the trench was in this case crossed from NE to SW at a speed of 7½ knots. The eastern side shows a regular gradient of 1 : 7,5 and could thus easily be recorded, while the western side over a horizontal distance of about 240 m rises steeply to a height of 260 m from the bottom, that is at a gradient of somewhat more than 1 :1, and returns no echo. In these and other similar analyses of echograms at great depths (6,000-10,000 m) in the Philippine Trench, a maximum spread from the perpendicular of 600 m has been calculated with, a spread of common occurrence in this area, but in many cases considerably less in other seas. For the plotting of the edge C in Fig. 9-B the weak echo first heard was used, corrected by -25 m for the oblique course of the sound.

The seabed is more irregular at the place where Section II crosses the trench (Fig. 10-A-B). The western side subsides here at an average gradient of 1 : 4.5, but the decline is irregular with several sloping surfaces or clefts towards the bottom of the trench, which incidentally here has a deeper channel along its middle. The eastern side, on the other hand, rises steeply to a small, isolated plateau or N-S ridge more than 1,000 m above the bottom.

Fig. 9-A. Photographic reproduction of echogram from passage across the deepest part of the trench, Section III, Plate I.

Fig. 9-B. Cross-section of the trench prepared on the basis of the echogram in Fig. 9-A. Exaggeration of vertical scale 2.5.



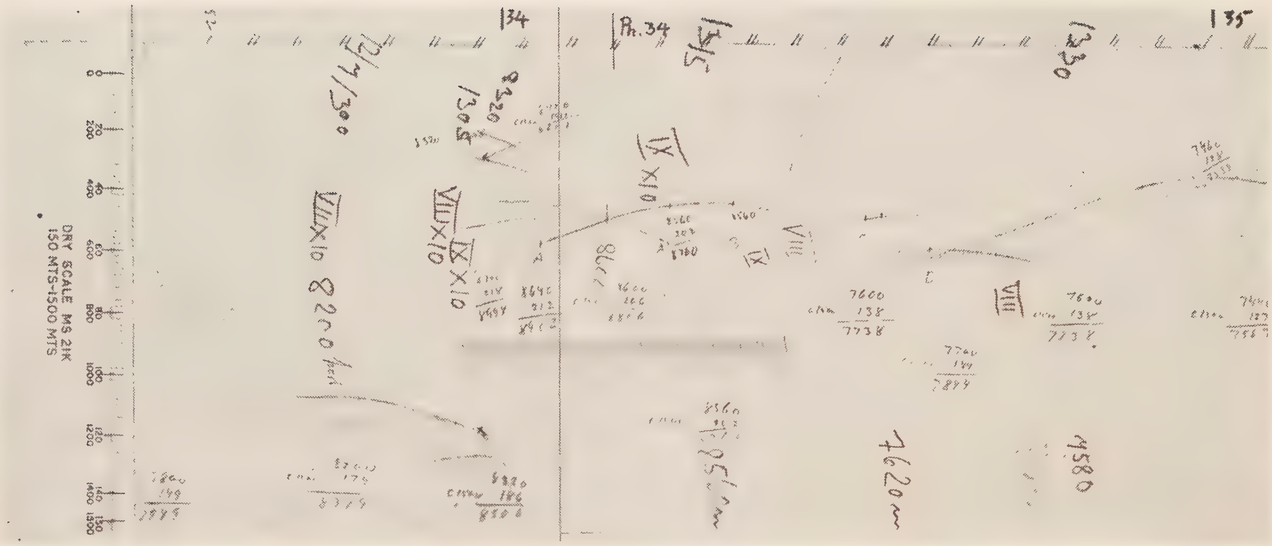


The width of this plateau cannot be determined with exactitude, but it is so narrow that the echo from it was only recorded at most 300-400 m from its edge.

The slopes of the bottom towards A are not too steep to give good echoes, but due to the spread of the beam the curves of the echogram intersect one another until 600 m from the middle of the trench. The lower ends of the intersecting curves were used as a basis for the calculation of the depth at A, and in this case regard was paid to the oblique course of the sound waves and a correction of -25 m was applied. The eastern slope B-A continues to the west of A as a narrow tongue or valley about 600 m into the western side and down to a depth of 86 m below A.

When the gradients of the sides are not too steep for the reception of an echo and the spread of the sound beam is of known and limited size, the profile of the bottom of the cleft may be reconstructed in the manner here used, but if the sides are steeper so that no echo is received, or if a directional sound wave is not used, but for instance sounding by detonation, the bottom of the channel cannot be reconstructed at all, or without any amount of accuracy. Thus, an expedition from Scripp's Institute in 1952-1953 took soundings in the Tonga Trench by detonation and measured a depth of 10,633 m. Fisher is, however, of opinion that the depth may be not less than 10,800 m and that the configuration of the sides may be different from that calculated (Fisher, 1954).

An echo section along the sides of the Philippine Trench may over short distances in many cases show a regular, continuous slope. The most common feature seems, however, to be that the slopes down towards the trench are irregular and heavily incised, as will be seen from Fig. 11 which shows part of the echogram recorded during the southward voyage along the western slope of the trench some distance to the south of the San Bernadino Strait. An exact analysis of the many curves would not be feasible,



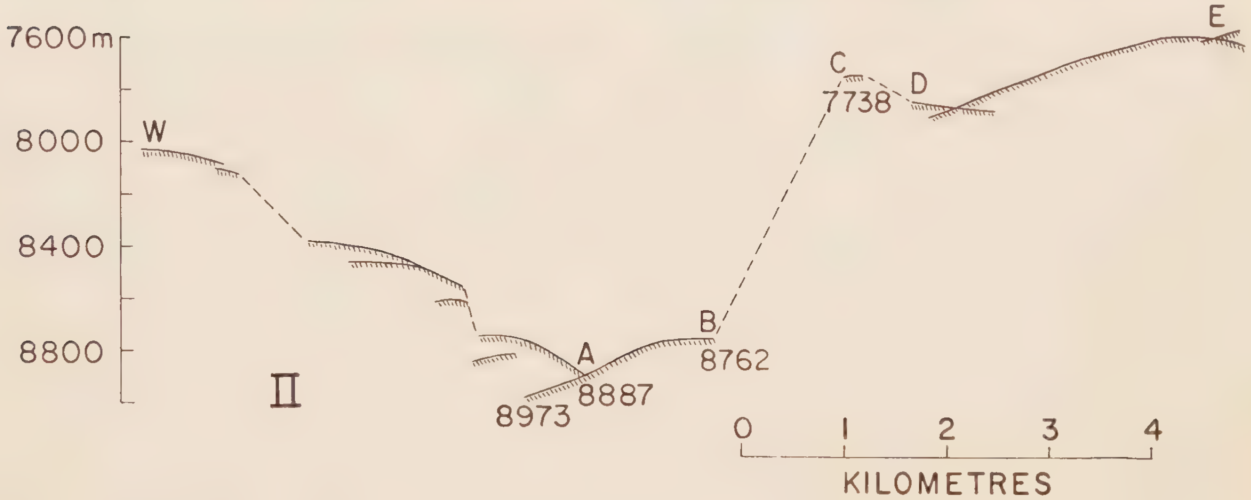


Fig. 10-A. Photographic reproduction of echogram from passage of the deepest part of the trench, Section II, Plate I.
Fig. 10-B. Cross-section of the trench prepared on the basis of the echogram in Fig. 10-A. Exaggeration of vertical scale 2.5.

nor would it serve any practical purpose. The echogram does, however, give some notion of the average depth and in particular a good picture of the jagged character of the slope.

ACCURACY OF POSITIONS OF OBSERVATIONS

The greatest difficulty in connection with an exact survey and plotting will no doubt always be encountered in the determination of the position of the ship and thus also of the sections. The distance from the middle of the trench to the shore averages about 40 nautical miles (75 km), so that in clear weather the highest points of the archipelago may be seen although they cannot be used for the purpose of fixing the position. There was no DECCA chain in the Philippines and the LORAN stations were so remote that they could not be used for a determination of the position with sufficient accuracy. Astronomical fixes must therefore be used as a basis for all positions, and as a consequence observations were taken on board the "GALATHEA" as frequently as possible and with the maximum care. While in most cases we may reckon that the inaccuracy in the determination of positions does not exceed ½-1 nautical mile, certain optical irregularities at times caused, particularly the determination of longitude to be difficult, so that subsequently the longitudes of the sections had to be corrected by other means. Despite the good weather we generally had the sky was often overcast so that whole days might pass without possibilities of obtaining a fix, and when later on we succeeded in getting an ob-

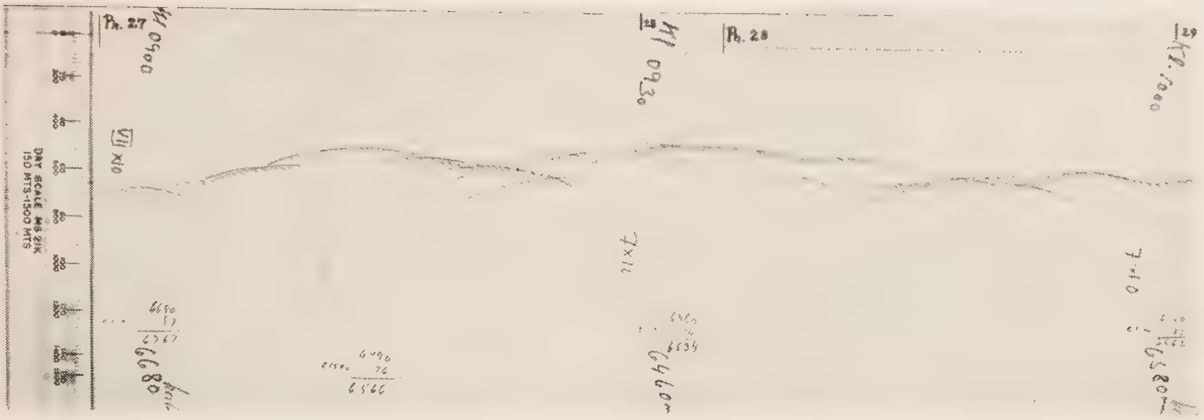


Fig. 11. Photographic reproduction of echogram from jagged slope along the western side of the trench.

servation it frequently appeared that the current had set the ship in a way different from that calculated, so that the intermediate dead-reckoning positions had to be corrected.

The current forms part of the trade drift and therefore mainly comes from the east, but off the Philippine Islands it curves and continues in a southerly direction, but both set and speed vary considerably, and a current of 1-2 knots is a very common phenomenon. Under such circumstances it is difficult to maintain the ship's position during work and also to keep a proper dead reckoning during passages.

Not only in the work on board but also in the preparation of the data collected the greatest possible care and criticism were therefore exercised, and we venture the opinion that although the positions of the sections and charts prepared in this treatise may be subject to correction, such corrections can be made only when new technical aids become available.

When on board the U.S. "CAPE JOHNSON" they measured the maximum depth of the trench (10,497 m), they counted on an inaccuracy in position of 3.5 miles (6.5 km), although the ship had proceeded to the position direct from shore and had radar communication with land until 4 hours before the soundings were taken and again 6 hours later fixed their position both by LORAN and an observation of the sun (Hess and Buell, 1950). Of necessity we must in the "GALATHEA" count on a similar or perhaps even greater inaccuracy on days with poor observation facilities, but now when all the echo sections have been worked out and compared with accurate fixes, we may take it that in general the inaccuracy of the data compiled will not exceed 1½ or 2 miles.

CROSS-SECTIONS OF THE TRENCH

Plates I-II

As the echo sounder was kept going throughout our stay over the Philippine Trench an exceedingly great number of echograms is available, and of these 26 of the best cross-sections are reproduced in Plates I and II. They have all been drawn with a vertical exaggeration of 3.7 (500 m vertically = 1 nautical mile horizontally). The parts of the sections drawn in full line correspond to the distances over which echoes could be received, whereas the stretches from which no echo could be heard are drawn in broken, straight lines.

As a consequence of the abovementioned difficulties in fixing positions, some of the sections were in the work done locally plotted in the charts in a wrong longitude. As, however, it must be presupposed that the deepest channel forms an entity and follows a reasonably regular course, the sections have been displaced in direction east-west, so that the deepest parts of all the sections will be found in a vertical line down across the plates.

Four of the most perfect sections (I, II, XI-XII and XXVI) have further in Fig. 12 been represented as blocks presumed to be resting on a plane surface at a depth of 10,000 m and spaced 70-95 nautical miles (130-175 km) apart.

Most of the cross-sections show the abovementioned configuration, namely, that the western slope passes down towards the bottom by many, small steps, whereas the eastern side has few but tall steps. Most of the sections between II and XI likewise show subsidence areas in the seabed to the east of the main trench, either branches of the main trench or isolated depressions, or a more or less continuous parallel trench.

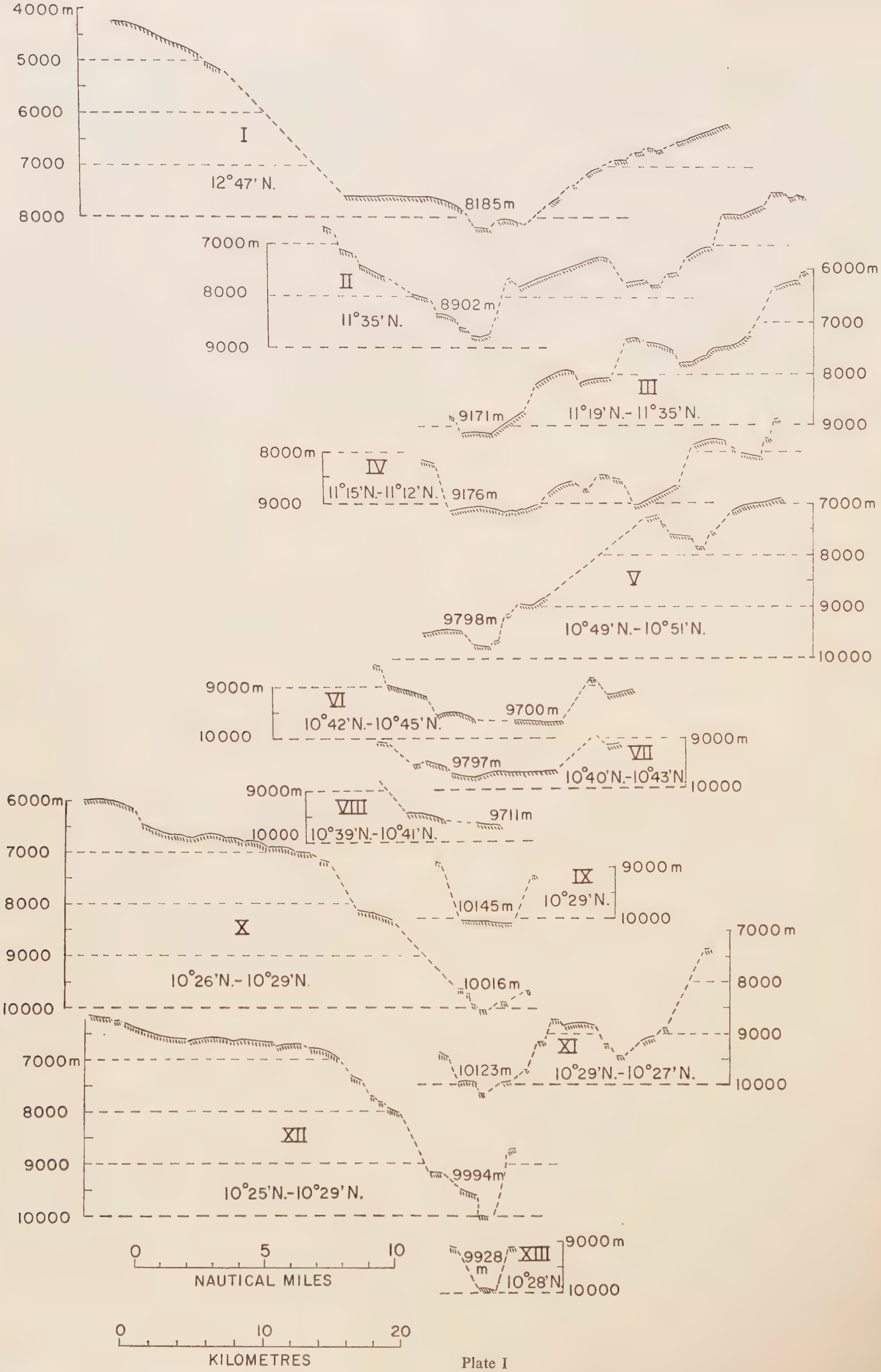

4000 m
5000
6000
7000
8000
I
12°47' N.
8185 m
7000 m
8000
9000
II
11°35' N.
8902 m
6000 m
7000
8000
9000
III
11°19' N.- 11°35' N.
9171 m
8000 m
9000
IV
11°15'N.-11°12'N.
9176 m
7000 m
8000
9000
10000
V
10°49' N.- 10°51'N.
9798 m
9000 m
10000
VI
10°42'N.-10°45'N.
9700 m
9000 m
10000
VII
10°40'N.-10°43'N.
9797 m
9000 m
10000
VIII
10°39'N.-10°41'N.
9711 m
9000 m
10000
IX
10°29'N.
10145 m
6000 m
7000
8000
9000
10000
X
10°26'N.- 10°29'N.
10016 m
7000 m
8000
9000
10000
XI
10°29'N.-10°27'N.
10123 m
7000 m
8000
9000
10000
XII
10°25'N.-10°29'N.
9994 m
9000 m
10000
XIII
10°28'N.
9928 m
0
5
10
NAUTICAL MILES
0
10
20
KILOMETRES

Plate I

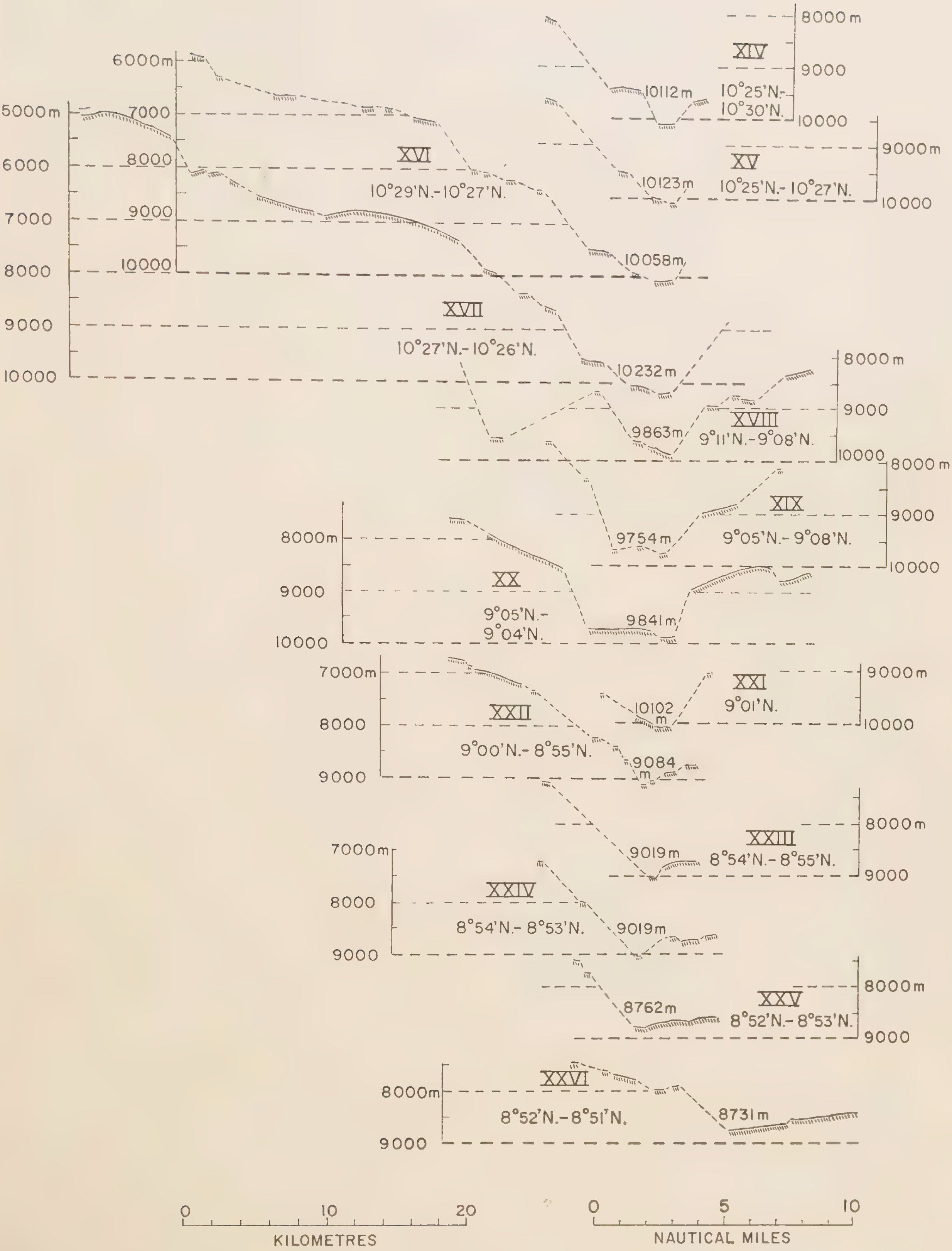

XIV
10°25'N.-10°30'N.
10112 m
8000 m
9000
10000
XV
10°25'N.-10°27'N.
10123 m
9000 m
10000
XVI
10°29'N.-10°27'N.
10058 m
6000 m
7000
8000
9000
10000
XVII
10°27'N.-10°26'N.
10232 m
5000 m
6000
7000
8000
9000
10000
XVIII
9°11'N.-9°08'N.
9863 m
8000 m
9000
10000
XIX
9°05'N.-9°08'N.
9754 m
8000 m
9000
10000
XX
9°05'N.-9°04'N.
9841 m
8000 m
9000
10000
XXI
9°01'N.
10102 m
9000 m
10000
XXII
9°00'N.-8°55'N.
9084 m
7000 m
8000
9000
XXIII
8°54'N.-8°55'N.
9019 m
8000 m
9000
XXIV
8°54'N.-8°53'N.
9019 m
7000 m
8000
9000
XXV
8°52'N.-8°53'N.
8762 m
8000 m
9000
XXVI
8°52'N.-8°51'N.
8731 m
8000 m
9000
0
10
20
KILOMETRES
0
5
10
NAUTICAL MILES

Plate II

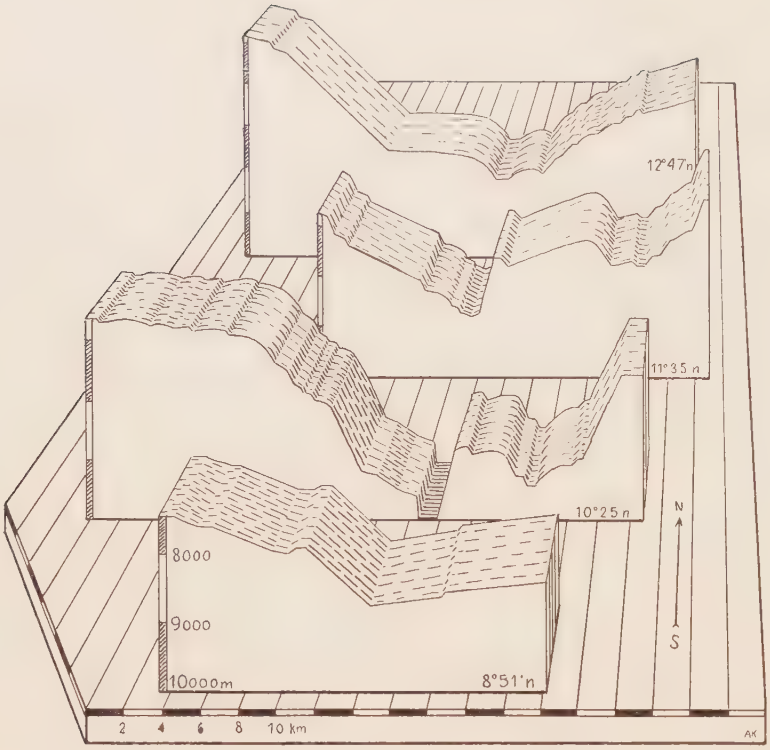


Fig. 12. 4 Sections of the bottom of the Philippine Trench.

BATHYMETRIC CHART OF THE PHILIPPINE TRENCH

Plates III-VI

Already when in 1907 the German survey vessel "Planet" for the first time ascertained the great depth in the Philippine Trench, so many soundings were taken as to make it possible to draw a depth chart which roughly gave a good idea of the location of the trench (Groll, 1912), and in many places depth curves from this first chart may still be used. To be true, by these first soundings no depths of more than 8,500-8,553 m were found, while already at an earlier time depths of 9,427 m and 9,636 m had been measured in the Kermadec Deep and the Marianas Deep, respectively. In 1912, the "Planet", however, in several places got soundings of more than 9,000 m, and thereby ascertained a better continuity along the trench. With its 9,788 m the Philippine Trench now assumed the position of the deepest place in the oceans.

During the "Emden"'s survey of the Philippine Trench in 1927 the work was concentrated on a rectangle between 9°38′ N, and 9°57′ N, in which 332 echo soundings were taken, 46 of which showed depths of more than 10,000 m. Thereby one of the deepest areas of the trench was localized, even if the deepest soundings (10,790 m and 10,830 m) which soon were recorded in literature were subsequently declared to be erroneous, inasmuch as they must be due to echoes from the sides of the trench (Maurer, 1937, Hess and Buell, 1950, Wüst, 1950-1951). Maurer and Wüst consider 10,400 m a more probable depth.

The soundings taken by the "Snellius" in 1930 (van Huystee, 1944) supplied a number of good soundings within the "Emden"'s area and to the south thereof, but no new record depth was found.

In 1944-1945 the "Cape Johnson" laid 4 sections across the trench, partly in the vicinity of the "Planet" and "Emden" deeps and partly somewhat more to the north, and in the northernmost of these sections the greatest depth so far known within this trench was found, – 10,497 ± 90 m, in 10°26.5′ N, 126°39′ E – by means of an echo sounder of a frequency of 18 kc and soundings taken every second mile registered by earphone.

The soundings taken by these expeditions have formed the most important basis of the charts as well as of the Monaco chart and the bathymetric charts published by the U.S. Hydrographic Office in 1946 (No. 5485) and the Japanese Hydrographic Office in 1953 (No. 6901) (Dietz, 1954). Roughly, they show the same picture of the Philippine Trench and none of them attempts to give details thereof.

The bathymetric chart given here (Plates III and IV-VI) has mainly been prepared on the basis of the configurations shown by the 26 cross-sections in

Plates I-II, and the corrected positions of these sections are plotted in the chart. In the drawing of the depth curves these sections have been supplemented by a very great number of other sections which are less perfect and the positions of which have in many cases been adjusted to conform to the 26 basic sections. The depth curves for 7,000 m and downwards are based almost solely on the observation data of the "GALATHEA", whereas the curves for 2,000, 4,000 and 6,000 m are based also on the existing charts.

From the chart as well as from the sections it appears that the trench roughly extends as a continuous subsidence through the entire area examined, i. e. across 4° of latitude, and that in almost the entire southern half of the area depths of about 10,000 m are to be found.

According to our observations, and thus shown in the chart, the northern end of the trench is about 15 nautical miles closer to land than shown in the American chart No. 5485. The position should be rather accurate inasmuch as the "GALATHEA" proceeded there direct from the San Bernadino Strait at a constant speed of 11 knots and obtained good fixes in the evening 5½ hours before the deepest channel was passed and also next morning 3½ hours after the passage. The speed of the current outside the strait may, however, have been wrongly estimated either by us or by the previous expeditions, so it must be left to some future expedition to try to solve this question.

From this northernmost section to section II in 11°35′ N we have only one long section in direction N-S intersecting the trench at a very acute angle, so the curves here have been roughly drawn on the basis of estimates, and no doubt present a more regular picture of the course of the trench than is actually the case. In Fig. 11, which originates from this very section, it was, however, mentioned that the sides in this place are of a very jagged nature.

South of 11°35′ N the trench becomes wider and deeper and seems to take a uniform course to about 10°45′ N. Over this distance the bottom is at a depth exceeding 9,000 m, and the sides show the characteristic features with terraces on the western slope and a secondary valley or depressions along the eastern side separated from the main trench by ridges of up to 500 m.

At 10°50′ N the bottom deepens to somewhat more than 9,700 m, but immediately to the south thereof the trench is wholly or partly interrupted by a crossing ridge projecting from the east and having a depth of less than 7,000 m. In this latitude several earthquakes have been registered inshore, so the possibility remains that this interruption of the trench is connected with a line of fracture in the crust extending out here from the shore (Repetti, 1931).

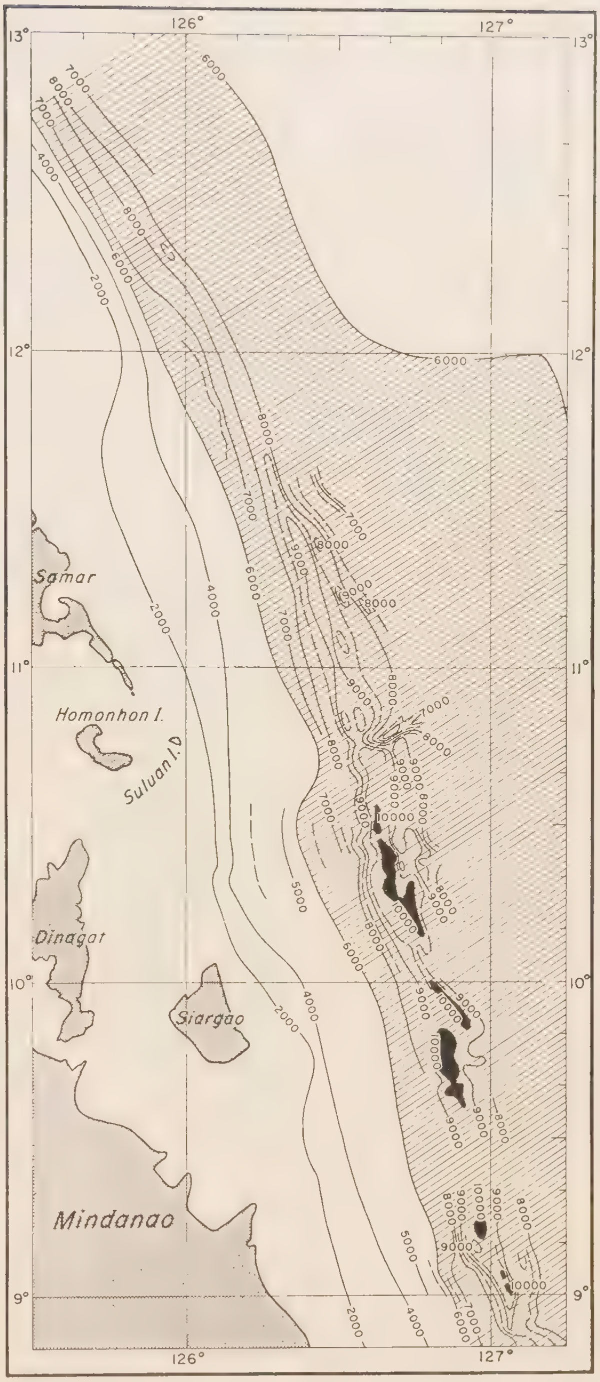


Plate III

Between 10°45′ N and 10°05′ N the central part of the trench is situated. In this place it is wider than in the northern part, and it was here the "CAPE JOHNSON" in July, 1945, obtained a sounding

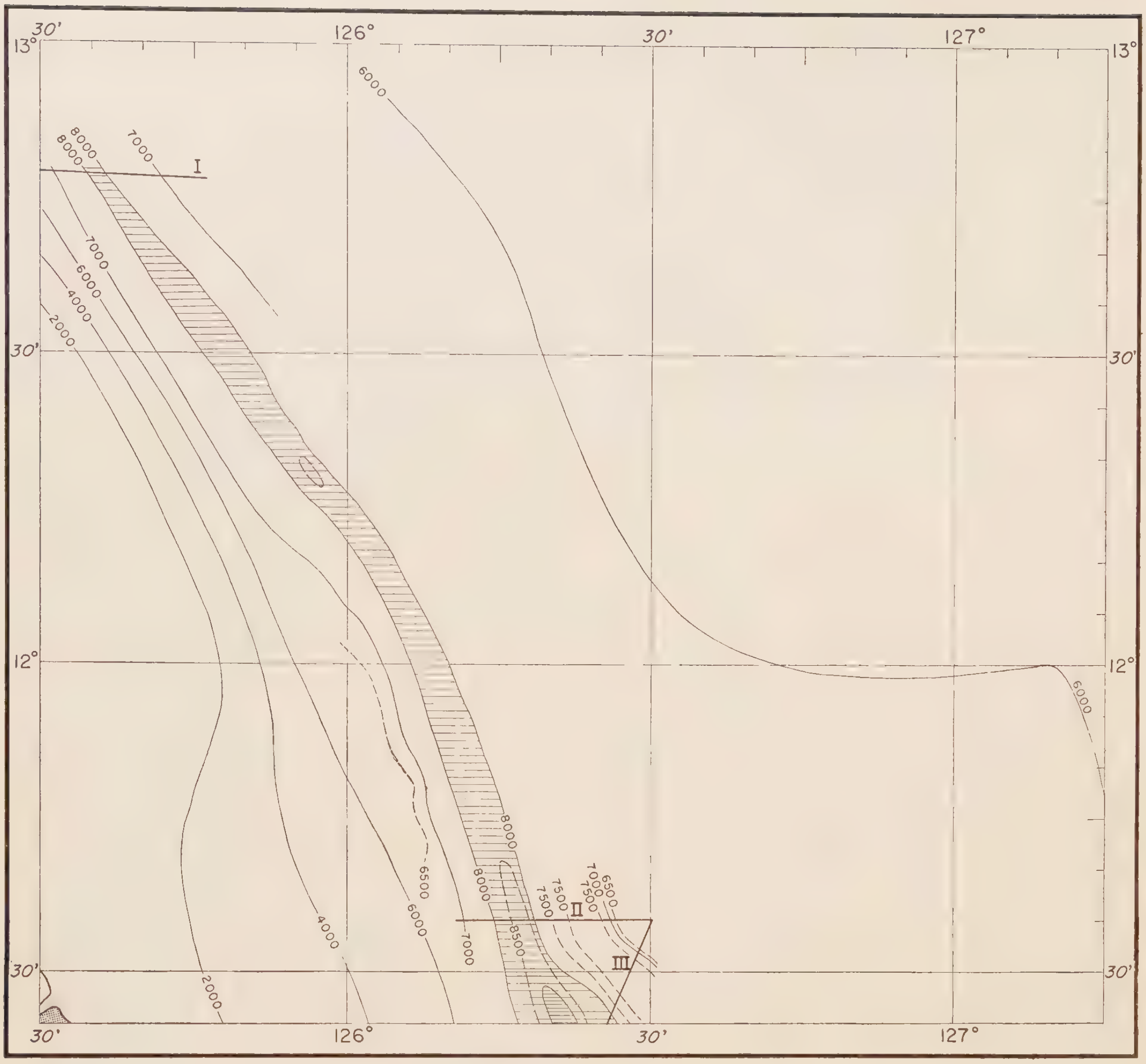


Plate IV

of 10,497 m. As the "GALATHEA" just about this position given by the "CAPE JOHNSON" found particularly good conditions for trawling, we made this our main working area and crossed it time and again. During such a crossing on July 23rd, 1951, in 10°23.8′ N, 126°40.5′ E we found the expedition's greatest depth, 10,265 m ± 45 m, i. e. in a position $3\frac{1}{2}$ miles south of that of the "CAPE JOHNSON". The area containing depths of more than 10,000 m has here at places a width of 2-3 miles, but in most places the deepest channel is quite narrow with widths of less than $\frac{1}{2}$ nautical mile. The bottom of the trench is amazingly flat and over long stretches shows uniform depths of 10,000 - 10,150 m, but the soft clay ground is amply strewn with gravel and stones which must have come from the sides and possibly have been carried out there by mud slides released by earthquakes. (Bruun & Kiilerich 1955).

As we crossed this area so many times, we must assume that we have also crossed the position given by the "CAPE JOHNSON". We did not, however, find the same great depth, but the possibility cannot be rejected that the 10,497 m sounding has been taken a short distance from the position given or in a depression of so small an extent that we have not happened to encounter it during any of our passages. There is thus no basis for either a confirmation or a rejection of the sounding taken by the "CAPE JOHNSON", and the possibility therefore remains that within or in the immediate vicinity of the area preferred by us for trawling a very restricted deep of 10,497 m may exist, and thus still must be re-

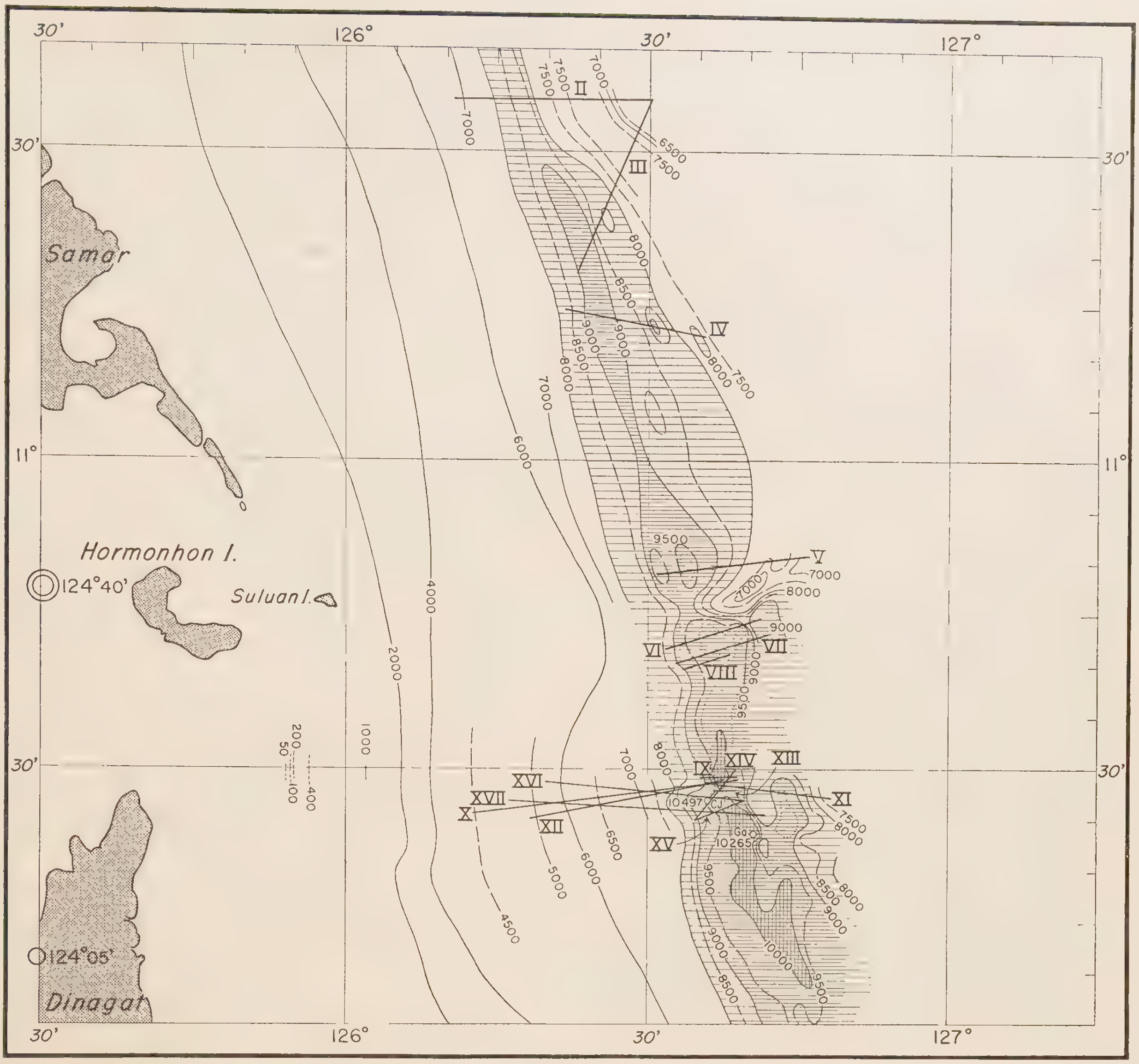

30'
126°
30'
127°
11°
Samar
Hormonhon I.
124°40'
Suluan I.
Dinagat
124°05'
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV
XV
XVI
XVII
10497
CJ
10265
1000
2000
4000
6000
7000
8000
9000
9500
10000

Plate V

cognized as the greatest depth of the Philippine Trench.

Slightly to the north of 10° N the trench again narrows and only a very narrow channel of a depth of about 9,500 m leads – possibly with minor interruptions – to the next section immediately to the south of 10°. It is here the "PLANET" and the "EMDEN" deeps are to be found, and here the "SNELLIUS" and the "CAPE JOHNSON" as also now the "GALATHEA" have searched for the great depth found by the "EMDEN" and concordantly found the greatest depths in this area slightly deeper than 10,100 m. The positions of these expeditions seem to be accurate and consistent, and consequently these soundings have been used extensively in the preparation of this part of the chart.

On the stretch from 9°40′ N to 9°12′ N we encountered so bad weather that the determination of the ship's position was very uncertain, and over long distances no echo could be registered. The latter feature would seem to indicate that the configuration of the bottom here is highly irregular, but as at several places echoes of short duration were received from depths of up to 10,150 m we may take it that by and large the trench continues also through this area and is connected with the deeps at about 9° N even if the data are insufficient to be plotted in the chart.

Within the southernmost area of the chart we found several minor areas with depths of about 10,000 m. Here the trench is of a different character from that farther to the north, there being no evident

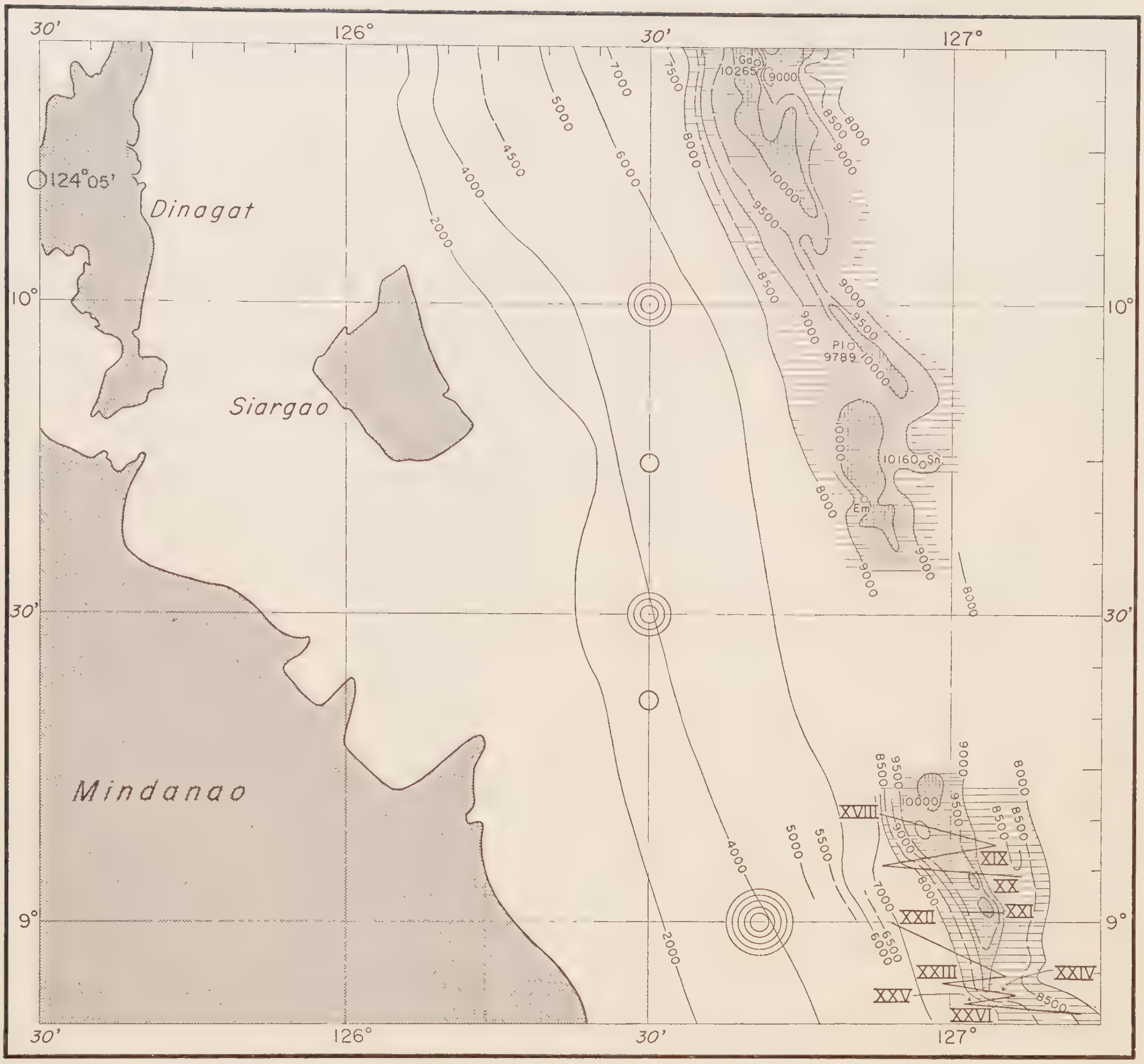

30'
126°
30'
127°
10°
30'
9°
Dinagat
Siargao
Mindanao
124°05'
10265
Ga
9000
P10
9789
10160
Sn
Em
10000
XVIII
XIX
XX
XXI
XXII
XXIII
XXIV
XXV
XXVI
2000
4000
4500
5000
5500
6000
6500
7000
7500
8000
8500
9000
9500
10000

Plate VI

demarcation to the east. To the south of 9° N the trench flattens and in our southernmost section in 8°51′ N no depths of more than 8,750 m were sounded.

EARTHQUAKE CENTRES ALONG THE PHILIPPINE TRENCH

The many earthquakes which occur in the Philippine Archipelago have in most cases their epicentres on the slopes leading down to the surrounding deeps. The epicentres of the 15 earthquakes which in the decade 1920-1929 occurred on the western slope of the part of the trench dealt with in this treatise, have been indicated in the chart by circles (according to Repetti, 1931). More than one epicentre in the same position is indicated by several circles inside each other. The possibility exists that there is a certain relation between the many earthquakes along southern part of the trench and the irregular topography of this part.

By this chart we have endeavoured to compile and publish as much as possible of the great material of observations to be found in the many hundred metres of echograms from the Philippine Trench collected by the "Galathea". Many deficiencies may be found in the chart and, no doubt, also errors, but we entertain the hope that it may form the basis for the work of later expeditions within this area and that some of the experiences gathered by us and mentioned in this treatise may benefit others.

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STEPHANOSCYPHUS

(SCYPHOZOA)

By P. L. KRAMP
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Numerous specimens of the scyphozoan polyps *Stephanoscyphus* were collected by the Galathea Expedition in 33 localities in the Atlantic, Indian and Pacific Oceans. Careful examination and measurements show that they all belong to one species, *Stephanoscyphus simplex* Kirkpatrick, with the exception of some few specimens from shallow water in the Macassar Strait and South China Sea, which I refer to *S. corniformis* Komai.

Provisionally we must retain *Stephanoscyphus* as a generic name for all the various species of scyphopolyps with a horny and annulated or rugose perisarc tube. We know that *S. mirabilis* Allman and *S. racemosus* Komai, which is probably the same species, give origin to coronate medusae of the genus *Nausithoë;* the medusae of the other species are unknown and may belong to different genera; but as long as we do not know the medusae, we must classify the polyps as belonging to one genus, *Stephanoscyphus*.

Young specimens of the medusa of *S. simplex,* ready for liberation, will be described below. These medusae evidently belong to the Coronatae; they are very similar to the young stages of *Nausithoë punctata,* but the generic and specific affinity cannot be stated.

The present large collection has enabled me to carry out a revision of the species with a solitary, unbranched tube. A very valuable account of all the species known up to now is given by E. LELOUP (1937). I have found, however, that some of the distinctive features of the species are due to individual variation. First of all, the presence or absence of internal chitinous processes in the tubes are of no specific importance, whereas the shape and structure of such processes may exhibit some characteristic features which justifiy a separation of species.

LELOUP's account comprises the following species:

With branched colonies: *S. mirabilis* Allman 1874 (= *Spongicola fistularis* Schultze 1877), *S. allmani* Kirkpatrick 1890, *S. racemosus* Komai 1936, and *S. komaii* Leloup 1937. I shall not enter into a discussion of the reliability of these species, since they are not represented in the present collection.

With solitary polyps: *S. striatus* (Vanhöffen 1910) and *S. sibogae* Leloup 1937. These, and possibly also *S. bianconis* Thiel 1936, are identical with *S. simplex* Kirkpatrick 1890, and this latter is a distinct species and not a synonym of *S. mirabilis* Allman as supposed by LELOUP. *S. corniformis* Komai 1936 is likewise an independent species as will be demonstrated below, and not a synonym of *S. mirabilis*.

The two species, *S. simplex* and *corniformis,* are characterized by their solitary tubes which are attached to the substratum by a small button-like pedal disk. I have seen several specimens of *S. corniformis* and nearly 1000 specimens of *S. simplex* and I may state with certainty that the solitary habit is an absulutely constant feature; the pedal disk never shows the slightest indication of producing stolonial outgrowths from which other polypoid individuals might be developed. In this regard these species are quite distinct from the stolonial colonies of *S. mirabilis* as described by ALLMAN. There is no reason to believe that the absence of stolons is due to the polyps being attached to objects with a clean surface and not embedded in sponges like *S. mirabilis* and *racemosus*. When occasionally a tube of *S. simplex* seems to carry one or more lateral branches, it is simply because one or more specimens have attached themselves to the tube of another specimen and chosen it as substratum. There is no organic communication between them. *S. simplex* and *corniformis* are purely solitary species.

S. striatus and *bianconis* differ from *simplex* and *corniformis* merely by the absence of internal processes. In a previous paper (KRAMP 1951 p. 124)

I described some specimens of *S. simplex* from deep water in the Atlantic Ocean and expressed the opinion that the internal processes "do not seem to be of specific importance", and this supposition is confirmed by the examination of the numerous specimens in the Galathea collection. In every locality I have found a great variability in the number of internal processes.

Also in other respects the specimens are very variable. The rings of the annulated tube may be more or less prominent, with more or less sharp edges, close together or more or less distant, and the longitudinal striation between the rings may be very distinct or only sligthly indicated.

The relation between *S. simplex*, which is a deep-sea species, and *S. corniformis*, which occurs in rather shallow water, will be discussed below.

Stephanoscyphus simplex Kirkpatrick

Pl. 1, figs. 1-11.

Stephanoscyphus simplex Kirkpatrick 1890 p. 14, Pl. 3 fig. 2.
Spongicola sp. Lo Bianco 1903 p. 269, Pl. 7 fig. 6.
Tubularia striata Vanhöffen 1910 p. 280, fig. 6.
Scyphistoma striatum Vanhöffen 1910, p. VII.
Stephanoscyphus bianconis Thiel 1936 p. 389, fig. 199 f.
In part *Stephanoscyphus mirabilis* Leloup 1937 p. 60.
Stephanoscyphus striatus Leloup 1937 p. 64.
Stephanoscyphus sibogae Leloup 1937 p. 67, fig. 43.
Stephanoscyphus simplex Kramp 1951 p. 123, Plate figs. 4-5.

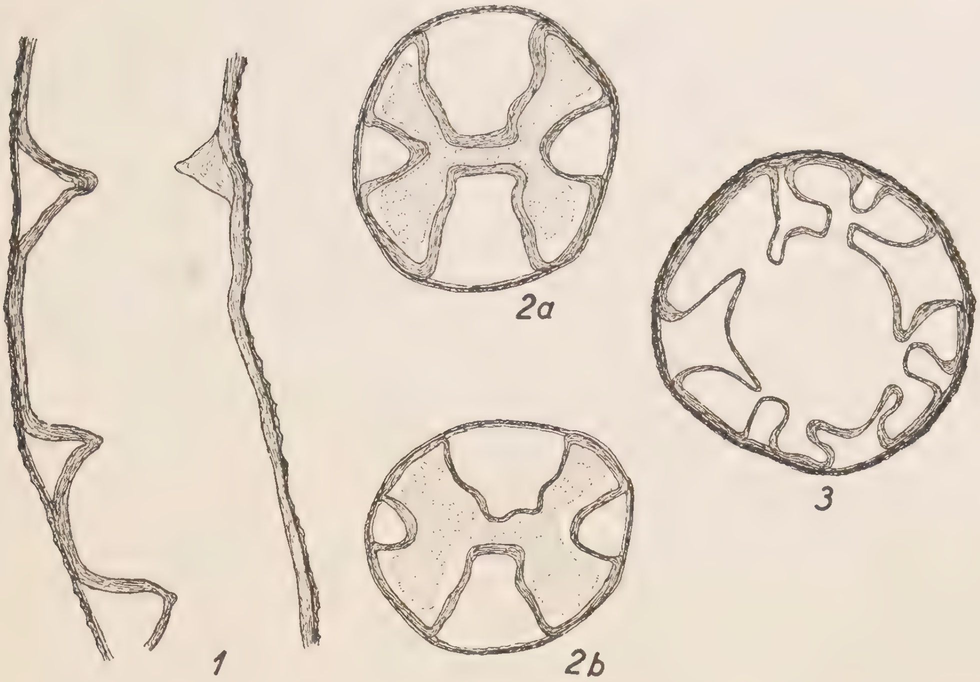
Description of the specimens in the Galathea collection

The chitinous tube. – In the majority of the numerous specimens observed the tube is less than 15 mm in length, but some few are up to 20 mm, one specimen even 28 mm long. It is evenly increasing in width from a very narrow base towards the terminal aperture. The ratio between the diameter of the aperture and the length of the tube is variable, usually between 0.10 and 0.16, exceptionally as much as 0.20-0.25; the average ratio is 0.13. The tube is generally slightly curved, though sometimes almost straight; irregular curvature may also occur. It is attached to the substratum by a small button-like pedal disk, usually circular in outline (Pl. 1, figs. 1-3), rarely slightly lobated. The pedal disk is hollow, traversed by irregular trabeculae (Pl. 1, fig. 4); the cavities contain prolongations from the living tissues of the polyp.

The external wall of the tube is annulated, divided into numerous rings, more or less prominent and with more or less sharp edges; the distance between the rings is likewise very variable as seen in the two tubes in figs. 1 and 2 which are from the same sample (stat. 471). A longitudinal striation is usually seen in the spaces between the rings, but also in this respects the variation is very considerable.

The wall of the tube consists of two layers (see text-figs. 1-3). The external layer is thin, and the annulation only comprises the outer surface of this layer, whereas its inner surface is smooth (see the longitudinal section in fig. 1). The inner layer is quite smooth, very thick in the lowermost portion of the tube, decreasing upwards and very delicate near the aperture. The growth of the tube evidently takes place in a similar way as that described by Komai (1935 p. 309) in *S. racemosus:* The uppermost part of the body of the polyp "which may be termed neck, has a thick epidermis, which contains numerous granular and clear gland cells . . . It is evident that the epidermis of this region plays an important part in the secretion of the periderm. The growth in length of the theca is apparently due to the secretion of new rings from this part, while the growth in thickness is brought about by the addition of new substance to the periderm by the more proximal part of the epidermis of the tube." Apparently the external, annulated layer of the chitinous tube is once and for all secreted by the "neck", whereas this part of the body is of very slight importance for the formation of the inner layer, which continually increases in thickness by secretion from glands in the entire length of the body-wall. This may account for the solidity of the lower portion and the delicacy of the upper portion of the tube.

The formation of the hollow internal processes is difficult to explain. They are figured in longitudinal section in text-fig. 1 and in transverse sections in text-figs. 2-3. The variation in number of these peculiar structures will be discussed below. They are arranged in distinct whorls of usually four large invaginations, placed cross-wise, and sometimes a small one in the middle of each space. The external layer does not take part in the formation of the invaginations, which are fissures in the internal perisarc layer expanding so as to form large, empty



Figs. 1-3. *Stephanoscyphus simplex.*
Fig. 1. Longitudinal section of the theca; stat. 279.
Fig. 2a-b. Transverse sections of the theca at the levels of two whorls of internal processes; stat. 279.
Fig. 3. Transverse section of a theca with small secondary internal processes between the four large ones; stat. 436.

cavities projecting into the central room of the tube (text-figs. 2 and 3). The shape of the processes is somewhat variable (see the figures), and they may project more or less deeply into the cavity of the tube; but in this species they have a broad or fairly broad base (in contradistinction to *S. corniformis,* see below), and they are frequently broader in transversal than in longitudinal direction (see Pl. 1, figs. 5 and 6, which present two successive whorls of one specimen, in which the tube has been cut open and spread out flat). The soft tissues of the body fill out the spaces between the processes and must attain a shape in accordance herewith. The number of whorls may amout to 14 but is usually much smaller, and some specimens have none at all. In one and the same specimen the whorls are not equidistant but separated by unequal distances. The distal portion of the tube is destitute of internal processes, but the distance from the uppermost whorl to the aperture of the tube is very variable.

Variation (Tables I-IV and text-figs. 4-5). Numerous specimens from different geographical areas and different depths have been examined in order to see, whether any correlations between various structural features might be pointed out. In all respects the variation is considerable, and it is evident that in all respects there is an even transition between specimens of both extremities, from which we may safely draw the conclusion that they all belong to one species.

Table I immediately shows that the limits of variation of the length of the tube and the number of whorls of internal processes is very nearly the same at all depths. We may be allowed, therefore, to draw general conclusions from the observations illustrated in the following tables.

Table II gives the ratio of the diameter of the terminal aperture and the length of the tube. It will be seen that in the vast majority of the specimens the ratio is between 0.10 and 0.16, whereas divergences beyond these limits are rare. I have thought of the possibility that the variation of the longitudinal striation might show a correlation with the width of the tube, so that a particularly distinct and dense striation might occur in tubes of particularly slender shape, but no such correlation can be discerned.

Table III and text-fig. 4 show, as might be expected, that the average number of whorls of internal processes is increasing with the length of the tubes, but the table also shows that within each group of length the number of whorls is very variable.

Table IV. With the increasing thickness of the walls of the tube the colour changes from a light yellowish shade to a more or less dark brown. Notes have been made on the shades of colour in numerous specimens. The results cannot be expressed in exact figures, but some notion of the significance of the colour may be obtained by means of the percentage number of specimens which may

Variation in **Stephanoscyphus simplex**

Table I. Length of tubes and number of whorls of internal processes in specimens from different depths.

Depth, m	580-1000	1000-2000	2000-3000	3000-4000	4000-5000	5000-6000	6000-7000
Number of specimens examined........	200	1	95	15	150	11	120
Length of tubes, mm	2-21	5	4-17	2-10	2-13	2-12	3-15
Number of whorls of internal processes .	0-13	5	0-8	0-9	2-14	0-7	0-13

Table II. Ratio of terminal diameter and length of tube, d/l.

d/l	0.08	0.10	0.12	0.14	0.16	0.18	0.20	0.22	0.24	average 0.13
Number of specimens	7	20	39	32	27	0	5	1	1	

Table III. Correlation between length of tubes and number of whorls of internal processes.

Number of specimens examined.....	4	12	9	14	17	17	8	8	5	2	2	2	2
Length of tubes, mm	3	4	5	6	7	8	9	10	11	12	13	14	15
Number of whorls	0	0-5	0-3	0-7	0-4	0-7	0-9	0-9	3-10	1-3	1-13	8	4-9
Average number of whorls	0.0	1.0	1.1	1.9	1.9	3.1	4.7	5.0	6.8	1.5	6.5	8.0	6.5

Table IV. Proportion of dark tubes to length of tubes and number of whorls of internal processes.

Average length of tubes, mm......	6.1	6.8	8.9	8.8	11.6	12.0
Number of whorls	0-1	2-3	4-5	6-7	8-9	10-13
Percentage number of dark tubes ..	12	22	44	91	100	100

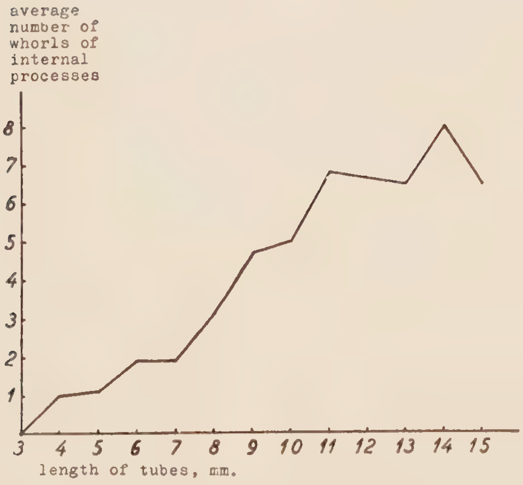


Fig. 4

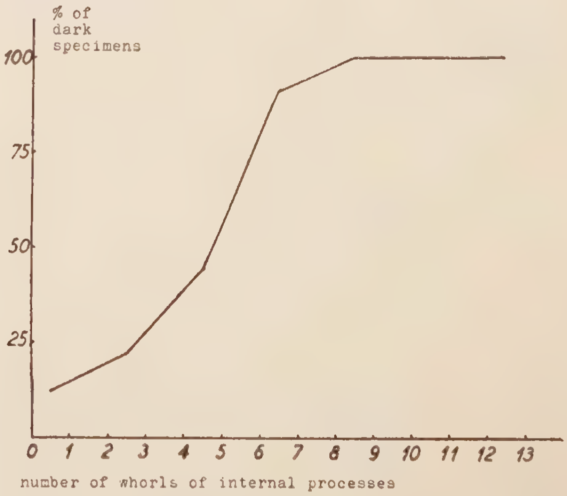


Fig. 5

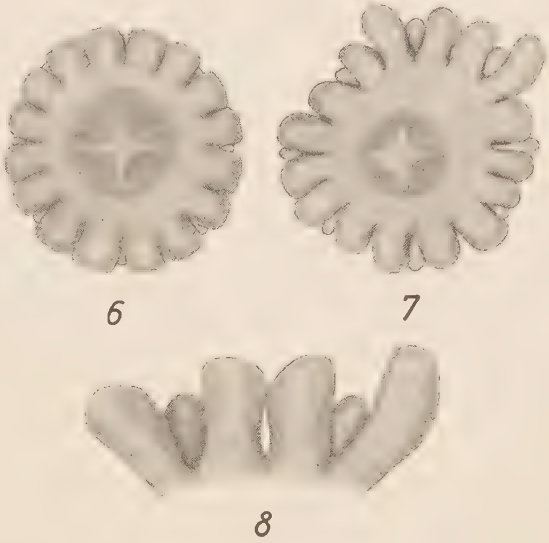
Variation in *Stephanoscyphus simplex*

be designated as "dark". Also in this respect the variation is considerable, but Table IV clearly shows that a dark colour is mainly found in the longest tubes. A particularly distinct correlation is shown between the colour and the number of whorls of internal processes; in the majority of the specimens with 6-7 whorls and in all specimens with more than 8 whorls the chitinous walls of the tube have a dark colour. This is further illustrated in the curve in fig. 5. That means that new whorls are continually added to the previous ones during the life of the polyp. The way of formation of the processes seems rather puzzling; it may have some connection with the strobilation, but since I have seen only one specimen in the act of producing medusae, I cannot state anything with certainty in this respect.

The soft tissues of the polyp. In the majority of the specimens hauled from the cold deep water through the warm surface layers the soft tissues were decomposed, usually quite destroyed, so that only the empty tubes were secured; but in one locality (stat. 279) the tissues were retained in some of the specimens, apparently in good condition, and I immediately preserved these specimens in Bouin's fluid. When later on I cut them into sections I found, however, that the fixation was very unsatisfactory. I ought perhaps to have cut open the tubes before the treatment with the fixative, though it is also possible that the tissues were already in a beginning state of decomposition. Some other specimens simply preserved in 70 % alcohol (stat. 436) were in a much better condition. They were not suitable for examination of minute histological details, but they give an impression of the general structure of the body (Pl. 1, figs. 7-11). Pl. 1, fig. 4 is an oblique section of the pedal disc, showing remnants of the tissues between the chitinous trabeculae. In the other figures the four taenioles are seen in transverse sections. They are quite distinct, each of them surrounded by a layer of muscular strands, and they contain numerous nuclei and some few nematocysts. In the section of the narrow pedicel of the polyp (Pl. 1, fig. 7) two of the taenioles are very thin, whereas the two others are rather wide even in this basal part of the body. In the parts between the whorls of internal processes (Pl. 1, figs. 8 and 9) the taenioles have a circular outline in transverse section, but at the levels of the processes they are more or less compressed and disfigured (Pl. 1, figs. 10 and 11). The endodermal epithelium of the stomach cavity is more or less mutilated. No successful sections have been made through the upper portions of the polyps, and tentacles are not observed.

The medusa. In one of the speimens at stat. 436 (among the Philippine Islands, 710 m) several small medusae had recently been liberated from the polyp and were found in the distal portion of the tube (Pl.1, fig. 3). They are all in the same stage of development, about 0.3 mm wide in their contracted condition (text-figs. 6-8). They have eight deeply cleft marginal lappets, each with a prominent sensory club as seen in the figures. The stomach may be discerned through the exumbrella. In all essential features they resemble newly liberated specimens of *Nausithoë punctata* and may belong to the same genus, of which three bathypelagic species are known, but it would be premature to put forward any opinion on their affinity, beyond the fact that they evidently belong to the order Coronatae.

The polyp had withdrawn into the lower portion of the tube as far as to the level of the uppermost of the four whorls of internal chitinous processes, which leads me to presume that the formation of these processes has some connection with the strobilation, but the tissues of the terminal part of the polyp were not in a condition suitable for anatomical examination. Unfortunately no other specimens were observed in the act of strobilation.



Figs. 6-8. Medusae of *Stephanoscyphys simplex* removed from the theca of a specimen from stat. 436, aboral views. In fig. 7 two of the marginal lappets are expanded.

Occurrence of Stephanoscyphus simplex
(see the map, fig. 9).

Stat. 99. Off Angola, 8°40′S. 11°10′E. 11. Dec. 1950. Depth about 2690 m. Yellowish clay. Bottom temp. c. 3.9°C.[1] 9 specimens on living lamellibranchs.

Stat. 182. Off South-East Africa, 33°28′S. 38°32′E. 27. Jan. 1951. Depth 5110-5340 m. Bottom temp. c. 0.7°C. 1 specimen, on pumice.

Stat. 196. Off Durban, 29°55′S. 31°20′E. 14. Feb. 1951. Depth 430 m. Bottom temp. c. 8.3°C. 40 specimens, on a calcareous tube.

Stat. 202. Off Durban, 25°20′S. 35°17′E. 21. Feb. 1951. Depth 590 m. Bottom temp. c. 7.4°C. 28 specimens, on living gastropods and one on a piece of slag.

Stat. 234. Off Mombasa, 5°25′S. 47°09′E. 10. March 1951. Depth 4800 m. Bottom temp. c. 1.8°C. About 110 specimens.

Stat. 279. East of the Maldive Islands, 1°00′N. 76°17′E. 8. April 1951. Depth 4330 m. Bottom temp. c. 1.3°C. About 60 specimens, on pumice.

Stat. 280. East of the Maldive Islands, 1°56′N. 77°05′E. 9. April 1951. Depth 4350 m. Bottom temp. c. 1.3°C. 17 specimens.

Stat. 281. South-west of Ceylon, 3°38′N. 78°15′E. 10. April 1951. Depth 3310 m. Bottom temp. ca. 1.8°C. About 20 specimens, partly on living lamellibranchs.

Stat. 299. Bay of Bengal, 17°10′N. 84°30′E. 24. April 1951. Depth 2820 m. Bottom temp. c. 1.7°C. About 90 specimens, on shells and pieces of coal and slag.

Stat. 314. Bay of Bengal, 15°54′N. 90°17′E. 3. May 1951. Depth 2600 m. Bottom temp. c. 1.7°C. 8 specimens.

Stat. 408. South China Sea, 12°47′N. 116°24′E. 4. July 1951. Depth 4330 m. Globigerina ooze. Bottom temp. c. 2.5°C. 5 specimens, on pebbles.

Stat. 423. East of Cebu, Philippines, 10°27′N. 124°18′E. 25. July 1951. Depth 810 m. Bottom temp. c. 10-11°C. About 60 specimens, on sponges *(Farrea)*, wooden pegs, and shells of living gastropods and lamellibranchs.

Stat. 436. East of Cebu, Philippines, 10°12′N. 124°14′E. 9. August 1951. Depth 710 m. Green mud. Bottom temp. c. 10-11°C. About 60 specimens, on stones, slag, pieces of wood and shells of gastropods and lamellibranchs.

Stat. 437. East of Cebu, Philippines, 10°19′N. 124°01′E. 10. August 1951. Depth 784 m. Bottom temp. c. 10-11°C. About 50 specimens.

Stat. 443. Mindanao Sea, 8°48′N. 124°09′E. 16. August 1951. Depth 1500 m. Mud. Bottom temp. c. 10°C. 4 specimens, on a calcareous tube and living lamellibranchs.

Stat. 450. Celebes Sea, 1°50′N. 119°20′E. 21. August 1951. Depth 4940-4970 m. Bottom temp. c. 3.8°C. 8 specimens, on stones.

Stat. 471. Sunda Trench, 10°26′S. 114°15′E. 10. Sept. 1951. Depth 2990-2810 m. Bottom temp. c. 1.7°C. 11 specimens.

Stat. 497. Banda Trench, 5°18′S. 131°18′E. 23. Sept. 1951. Depth 6490-6650 m. Soft clay. Bottom temp. 3.6°C. 32 specimens, on polychaet tubes.

Stat. 574. Tasman Sea, 39°45′S. 159°39′E. 18. Dec. 1951. Depth 4670 m. Bottom temp. c. 1.2°C. 21 specimens.

Stat. 601. Tasman Sea, 45°51′S. 164°32′E. 14. Jan. 1952. Depth 4400 m. Bottom temp. 1.15°C. 16 specimens.

Stat. 626. Tasman Sea, 42°10′S. 170°10′E. 20. Jan. 1952. Depth 610 m. Globigerina ooze. Bottom temp. c. 8°C. 20 specimens.

Stat. 650. Kermadec Trench, 32°20′S. 176°54′W. 15. Jan. 1952. Depth 6620-6730 m. Clay with pumice. Bottom temp. 1.3°C. About 50 specimens, on pebbles.

Stat. 651. Kermadec Trench, 32°10′S. 177°14′W. 16. Feb. 1952. Depth 6960-7000 m. Clay with pumice. Bottom temp. 1.3°C. About 45 specimens.

Stat. 653. Kermadec Trench, 32°09′S. 176°35′W. 17. Feb. 1952. Depth 6180 m. Clay with pumice. Bottom temp. 1.3°C. 35 specimens.

Stat. 654. Kermadec Trench, 32°10′S. 175°54′W. 18. Feb. 1952. Depth 5850-5900 m. Clay with pumice. Bottom temp. 1.2°C. 15 specimens, on pumice.

Stat. 661. Kermadec Trench, 36°07′S. 178°32′W. 23. Feb. 1952. Depth 5340 m. Bottom temp. 1.1°C. 4 specimens.

Stat. 663. Kermadec Trench, 36°31′S. 178°38′W.

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[1] Some of the temperatures are derived from observations in neighbouring localities.

24. Feb. 1952. Depth 4410 m. Sandy clay. Bottom temp. c. 1.2°C. 1 specimen, on a living lamellibranch.

Stat. 664. Kermadec Trench, 36°34′S. 178°57′W. 24. Feb. 1952. Depth 4540 m. Clay and pumice. Bottom temp. 1.1°C. 7 specimens, on living lamellibranchs, and on pumice.

Stat. 716. Off Nicaragua, 9°23′N. 89°32′W. 6. May 1952. Depth 3590 m. Dark clay. Bottom temp. 2.0°C. 11 specimens, on living lamellibranchs.

Stat. 724. Gulf of Panama, 5°44′N. 79°20′W. 12. May 1952. Depth 3190-2950 m. Dark clay and stones. Bottom temp. 2.0°C. 3 specimens.

Stat. 726. Gulf of Panama, 5°49′N. 78°52′W. 13. May 1952. Depth 3670 m. Clay. Bottom temp. c. 2.0°C. 1 specimen, on pumice.

Previous records

Atlantic Ocean: 56°11′N. 37°41′W., 2650 m (Kirkpatrick 1890). 28°25′N. 61°05′W. to 28°05′N. 60°49′W., 5500-5987 m; 24°12′N. 63°23′W. to 24°28′N. 63°18′W., 5850-5860 m; 2°26′N. 39°26′W. to 2°24′N. 39°12′W., 4474-4430 m (Kramp 1951). Near the Azores, 38°20′N. 28°04′45″ W., 1500 m; 38°35′30″N. 28°05′45″W., 1250 m (Leloup 1937).

Mediterranean: Near Capri, Italy, 950-1000 m (Lo Bianco 1903, Thiel 1936).

Indian Ocean: Somali Coast, 6°19′N. 49°32′5 E., 1079 m (Vanhöffen 1910).

Antarctic Ocean: about 65°S. 85°E., 2450 m (Vanhöffen 1910).

Malayan Archipelago: North of Soembawa, 794 m (Leloup 1937).

Horizontal distribution

As will be seen from the lists above, our knowledge of the geographical distribution of *Stephanoscyphus simplex* has been greatly augmented by the collections of the Galathea Expedition. The localities in the Atlantic Ocean are still few and scattered. The occurrence in the Indian sector of the Antarctic Ocean *(S. striatus* Vanhöffen) may seem very isolated but is easily explained by the hydrographical conditions which will be discussed below. In the tropical parts of the Indian Ocean it was taken only once before, but the "Galathea" found it in

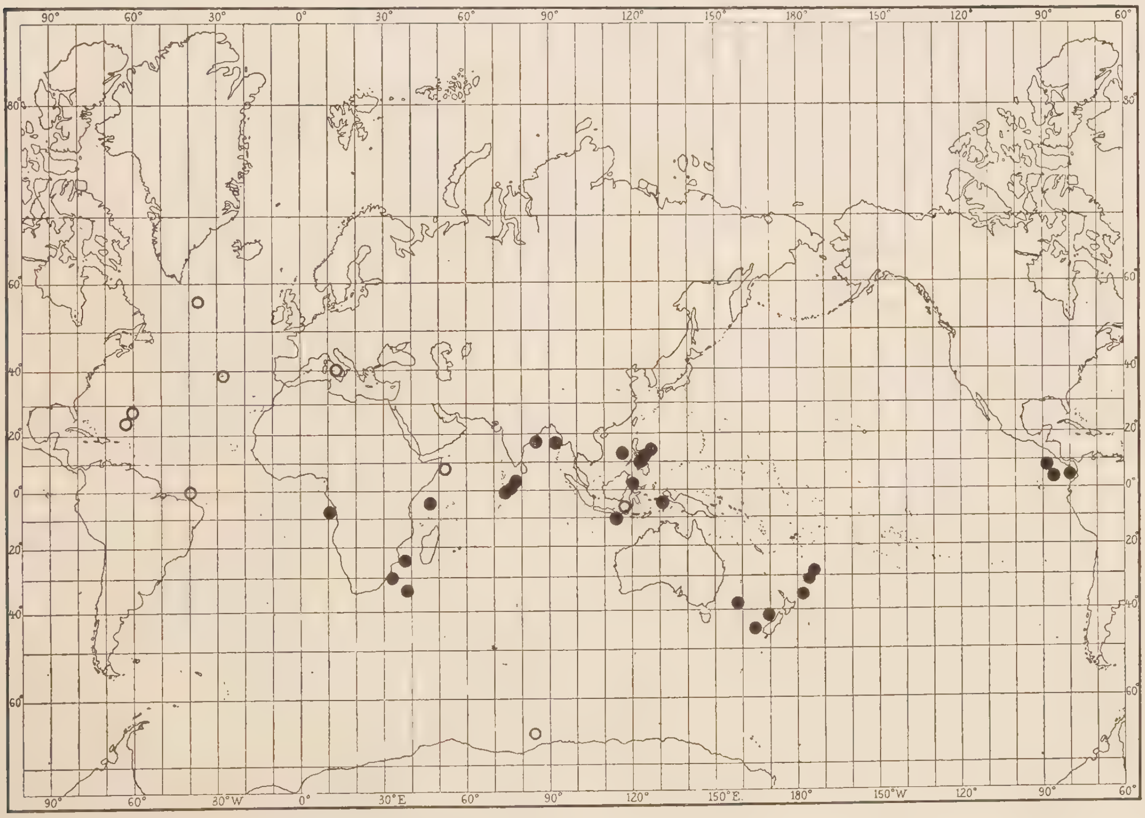


Fig. 9. Geographical distribution of *Stephanoscyphus simplex*. ● Localities where the species was collected by the "Galathea" Expedition. ○ Previous records.

Table V. *Stephanoscyphus simplex.* General survey of the vertical distribution and relation to temperature.

Depth, m	Temperature, °C.							Total
	< 1°	1-2°	2-3°	3-4°	4-6°	6-10°	> 10°	
430- 500						**1**/6		**1**/6
500-1000					**1**/?	**2**/48	**3**/170	**6**/218 +
1000-2000					**2**/?	**1**/?	**1**/4	**4**/4 +
2000-3000	**1**/?	**3**/109		**2**/9 +				**6**/118 +
3000-4000		**3**/34						**3**/34
4000-5000		**8**/233	**1**/5					**9**/238
5000-6000	**1**/1	**2**/19	**2**/4	**1**/8				**6**/32
6000-7145		**3**/130		**1**/32				**4**/162
Total.	**2**/1 +	**19**/525	**3**/9	**4**/49 +	**3**/?	**4**/54 +	**4**/174	
Grand total . ..	**28**/584 +				**7**/54 +		**4**/174	

Fat types: number of localities.
Light types: approximate number of specimens.

eleven localities from the east coast of Africa to the Java Deep. It was more or less abundant in six localities in the Malayan Archipelago, from where it was recorded only once before *(S. sibogae* Leloup). Moreover it was taken in three localities in the Tasman Sea and in seven of the hauls made in the Kermadec Trench, usually in considerable number. Of particular interest is the occurrence in the eastern tropical Pacific, where several specimens were found in three localities which were inhabited by an extraordinarily rich fauna of many other kinds of animals. *Stephanoscyphus simplex* thus seems to have an almost cosmopolitan distribution in the deep parts of all the oceans, except in the arctic basins.

Vertical distribution and relation to temperature

The total extent of vertical distribution of *Stephanoscyphus simplex* is very considerable, ranging from 430 to 7000 m at temperatures from slightly above 0° to 10 or 11°C, perhaps even to 13°, if the Mediterranean form *S. bianconis* belongs to the same species. There is no doubt, however, that *S. simplex* has its principal occurrence in the abyssal region at temperatures below 4°, from which it may descend into the hadal and, under certain conditions, ascend into the bathyal region, where it is exposed to higher temperatures.

A general survey of the occurrence is given in Table V comprising all records known up to now, including those derived from previous literature. For each depth and temperature is given the number of localities (fat types) and the entire number (actual or approximate) of specimens found in these localities (light types). The number of specimens taken in a single haul with the trawl or dredge is, of course, rather accidental and may not be considered as a reliable expression of the abundance of the species in the locality in question. Nevertheless, the total number found under equal conditions (depth and temperature) may serve to give a general impression of the multitude as compared with the multitude under other conditions.

It immediately appears from the table that by far the most catches are from depths exceeding 2000 m and temperatures below 4° (28 localities with nearly 600 specimens, of which 19 localities with more than 500 specimens at temperatures between 1 and 2°). The considerable number of specimens found in the four localities with the highest temperature (above 10°) needs special consideration. The predominance in the deep, cold waters is evident.

At any rate, one must bear in mind that shallow and intermediate depths are much more thoroughly investigated than the deep-sea areas. Were the species equally common at intermediate depths, as compared with the abyss, it would invariably have been found there in much greater quantities.

It is also evident that this species prefers low temperatures, but it does not occur in shallow water, even if the temperature is low. It must therefore be designated as a predominantly stenobathic species. Its preference of low temperatures also marks it as a species with a low temperature preference, but in this regard it is more adaptive than many other abyssal animals, since it may occur at temperatures several degrees above the optimal.

Origin[1]	Locality	Depth	Temp.	Number of specimens
"Gauss"	Antarctis	2450 m	0-0.2°	unknown
G. St. 182	S. E. of Africa	5110-5340 m	0.7°	1
"Albatross"	N. E. of Brazil	4474-4430 m	1.3°	3
G. St. 279	E. of Maldive Isls.	4330 m	1.3°	60
G. St. 280	–	4350 m	1.3°	17
G. St. 574	Tasman Sea	4670 m	1.2°	21
G. St. 601	–	4400 m	1.15°	16
G. St. 650	Kermadec Trench	6620-6730 m	1.3°	50
G. St. 651	Kermadec Trench	6960-7000 m	1.3°	45
G. St. 653	–	6180 m	1.3°	35
G. St. 654	–	5850-5900 m	1.2°	15
G. St. 661	–	5340 m	1.1°	4
G. St. 663	–	4410 m	1.2°	1
G. St. 664	–	4540 m	1.1°	5
G. St. 234	off Mombasa, E. Africa	4800 m	1.8°	110
G. St. 281	S. W. of Ceylon	3310 m	1.8°	20
G. St. 299	Bay of Bengal	2820 m	1.7°	90
G. St. 314	–	2600 m	1.7°	8
G. St. 471	Sunda Trench	2990-2810 m	1.7°	11
G. St. 716	off Nicaragua, E. Pacific	3590 m	2.0°	11
G. St. 724	Gulf of Panama –	3190-2950 m	2.0°	3
"Albatross"	W. Atlantic	5500-5987 m	2.1°	3
–	–	5850-5860 m	2.1°	1
G. St. 408	South China Sea	4330 m	2.5°	5
Kirkpatrick	N. Atlantic	2650 m	3°	unknown
G. St. 99	off Angola, W. Africa	2690 m	3.9°	9
G. St. 450	Celebes Sea	4940-4970 m	3.8°	8
G. St. 497	Banda Trench	6490-6650 m	3.6°	32
Prince of Monaco	Azores	1500 m	5°	1
–	–	1250 m	6°	1
"Siboga"	Flores Sea, Indonesia	794 m	5°	several
G. St. 202	off Durban, S. E. Africa	590 m	7.4°	28
G. St. 196	off Durban, S. E. Africa	430 m	8.3°	40
G. St. 626	W. of New Zealand	610 m	8°	20
G. St. 423	E. of Cebu, Philippines	810 m	10-11°	60
G. St. 436	– –	710 m	10-11°	110
G. St. 443	Mindanao Sea, –	1500 m	10°	4

[1] G. – "Galathea".

Table V gives only a rough outline of the occurrence of the species. The above complete list of the available records allows a more detailed analysis. In this list the localities are grouped according to the bottom temperatures. Some of these are actual observations, others are estimated from observations in neighbouring localities. In some instances the number of specimens is likewise approximate.

Occurrence below 1°C. – In very cold water, below 1°, the species was found by the German South Polar Expedition near the Indian sector of the Antarctic Continent ("*Tubularia striata*" Vanhöffen). Observations of the bottom temperature in this locality are not available to me, but from a not very distant "Discovery" station we may presume that at the depth of 2450 m, where the polyp was taken, the temperature has been slightly above 0°. The icy cold antarctic bottom water moves downwards along the slope of the continent and is overlayered by the "warm deep water" penetrating southwards from the Indian Ocean, and the locality, where the polyp was found, must be in the lower part of this body of water. "Galathea" stat. 182 is south-east of Africa, depth 5110-5340 m, where the temperature of the bottom, 0.7°, is influenced by the antarctic bottom water moving towards the east and north.

1-2°. – Among the 19 localities with temperatures between 1 and 2° is one from the western Atlantic; the others are scattered across the Indian and Pacific Oceans at depths between 2600 and 7000 m, and in several of these localities the polyps were taken in considerable numbers. The three localities with slightly higher temperatures, 2.1-2.5°, may conveniently be discussed in this same connection; two of them are in the deep western part of the Atlantic Ocean, between 5500 and nearly 6000 m ("Albatross") the third in the South China Sea, 4330 m. These extensive areas constitute the principal habitat of the abyssal species *S. simplex*. In the Kermadec Trench it was found to descend somewhat into the hadal region, as far down as 7000 m, and it was even fairly abundant in these great depths ("Galathea" stat. 650-653). Presumably, however, it is not a regular inhabitant of the hadal region (the depths exceeding 6000 m in the trenches); it was not taken in the two deepest hauls in the Kermadec Trench, 7630 and 8200-8300 m, and it was completely absent in the New Britain Trench where three hauls were made, all of them at depths exceeding 8800 m, and in the Philippine Trench, where no hauls were made in less than 10000 m. On the other hand, it might have been expected to occur in the Sunda Trench south of Java, where several hauls were made between about 3000 and 7300 m, but it was only taken in one of these hauls, the shallowest one, 2990-2810 m (stat. 471). Numerous animals belonging to the abyssal region have a cosmopolitan distribution, and this also applies to *S. simplex*. But since apparently it does not descend very far into the hadal regions, it does not contribute to a comparison between the hadal faunas of the different trenches.

3-4°. – *S. simplex* is still rather plentiful in the uppermost part of the abyssal region, at 3-4°, from which four records are known, two of them in the Atlantic Ocean, depth 2650-2690 m. The two others are from considerable depths, 4940-6650 m, in the Celebes and Banda Seas (stat. 450 and 497), yet at comparatively high temperatures, 3.8 and 3.6° respectively.

4-6°. – Records from areas with temperatures between 4 and 6° are very scanty; a few specimens have been found in two localities in the Atlantic near the Azores, 1250-1500 m, temp. about 6° and 5°. An interesting record is that from the Flores Sea north of the Indonesian island Soembawa, where the "Siboga" Expedition found several specimens ("*S. sibogae*" Leloup); the depth was only 794 m, the temperature about 5°. These records are interesting in so far as they establish a connection between the occurrences of the species in the abyssal region with temperatures below about 4° and the remarkable catches at much higher temperatures.

More than 7° but less than 10°. – Several specimens were found at stat. 202 off the south-eastern coast of Africa, 590 m, 7.4°, some few also at the neighbouring stat. 196, where the depth was only 430 m and the temperature as high as 8.3°. Further north, off Somaliland, the "Valdivia" Expedition found the same species at 1079 m, 8.2°. Under similar conditions it was found off the west coast of New Zealand, "Galathea" stat. 626, 610 m, temperature about 8°.

Above 10°. – Still more peculiar is the considerable abundance in which it occurred at the stations 423, 436, 437 and 443. All these are in the inland waters among the Philippine Islands at depths between 710 and 1500 m, where the temperature at the bottom is about 10-11°.

One might suspect that the specimens found in these comparatively warm bodies of water belonged to another species. Morphologically, however, they cannot be distinguished from abyssal specimens and, as mentioned above, specimens of the same appearance have been observed at intermediate temperatures connecting the high degrees among the Philippines with the low temperatures in the abyssal region.

Now, all these coastal areas, along the shelf of the East-African coast as well as in the sounds and basins between the Philippine Islands, are known to be inhabited by a very rich fauna. The nutritive conditions are certainly very favourable, and that may be the reason why an abyssal species like *S. simplex* is able to live and propagate in spite of the high temperatures prevailing there. High temperatures demand a vivid metabolism which can only be fulfilled, when considerable amounts of food are available.

Thus a closer analysis confirms the supposition that *Stephanoscyphus simplex* is a preferably abyssal species with a low temperature preference, but under certain conditions, especially under favourable food conditions, adaptive to the somewhat higher temperatures of the bathyal regions.

Stephanoscyphus corniformis Komai

Pl. 1, figs. 12-13.

Stephanoscyphus corniformis Komai 1936 pp. 175-183, figs. 1-4
in part *Stephanoscyphus mirabilis* Leloup 1937 p. 60

This species, which occurs in rather shallow water, is very similar to *S. simplex,* but differs from it in some respects. It was thoroughly described by KOMAI (1936), and some of the specimens recorded by LELOUP (1937) as belonging to *S. mirabilis* Allman most probably belong to the same species.

During the "Galathea" Expedition 10 specimens of *S. corniformis* were taken in the Macassar Strait (stat. 451); some others, from shallow water in the South China Sea (stat. 404), presumably also belonged to this species, but unfortunately the specimens have disappeared. Moreover the Danish "Atlantide" Expedition collected 7 specimens in the Gulf of Guinea.

Material:

"Atlantide" stat. 85. Gulf of Guinea, 5°37′N. 0°38′E. 30.I.1946, 50 m.

"Galathea" stat. 404. South China Sea, 5°09′N. 106°47′E. 30.XII.1951. 63 m. On a coral and a gastropod shell.

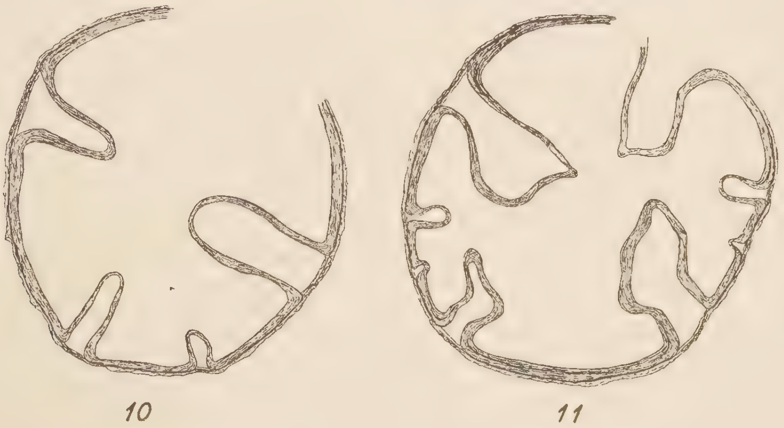
"Galathea" stat. 451. Macassar Strait, 1°25′S. 117°05′E. 23.VIII.1951. 60 m. On lamellibranch shells.

Remarks on the specimens.

S. corniformis is a solitary polyp attached to solid objects by means of a small button-like pedal disk. The tube is more or less curved, evenly increasing in width from a very narrow base to the terminal aperture. The length of the tube is usually less than 16 mm, but two of the specimens from the Macassar Strait are 22 and 24 mm in length. In the specimens 10-16 mm long the aperture is 0.8-1.1 mm wide, the ratio between the diameter af the aperture and the lenght of the tube varying between 0.06 and 0.10, average 0.075. The two largest specimens have a comparatively narrow aperture: length 22 mm, aperture 0.9 mm, ratio 0.04; length 24 mm, aperture 1.3 mm, ratio 0.054. Evidently, therefore, the tubes of this species are generally more slender than in *S. simples.*

The annulation and the longitudinal striation of the tube differ in no essential way from those in *S. simplex;* the edges of the rings are usually rather prominent and sharp.

The most important distinguishing feature between the two species is the shape of the internal chitinous processes. All the specimens of *S. corniformis* examined by me have several sets of these structures. Eash set consists of a whorl of four processes placed approximately at the same level, and frequently a number of additional, much smaller processes more or less irregularly scattered between the four primary ones (text-figs. 10-11, Pl. 1, figs. 12-13). In one very small specimen, 3 mm long, there is only one whorl, in the others the number varies between 3 and 9. In the Japanese specimens described by KOMAI the number of whorls was 7-10. In contradistinction to *S. simplex,* in which the processes have a broad base and frequently are broader in transversal than in longitudinal direction (see above, p. 3), the processes in *S. corniformis* are elongated in the longitudinal direction of the tube and have a narrow, almost slit-shaped base (see the figures, particularly, Pl. 1, fig. 13 which is an internal view of a part of the tube of a specimen from the Gulf of Guinea, cut open and spread out flat). KOMAI very adequately compared these processes in *S. corniformis* with the thorns of a rose.



Figs. 10-11. *Stephanoscyphus corniformis;* "Atlantide" stat. 85. Transverse sections of the theca at the levels of two whorls of internal processes.

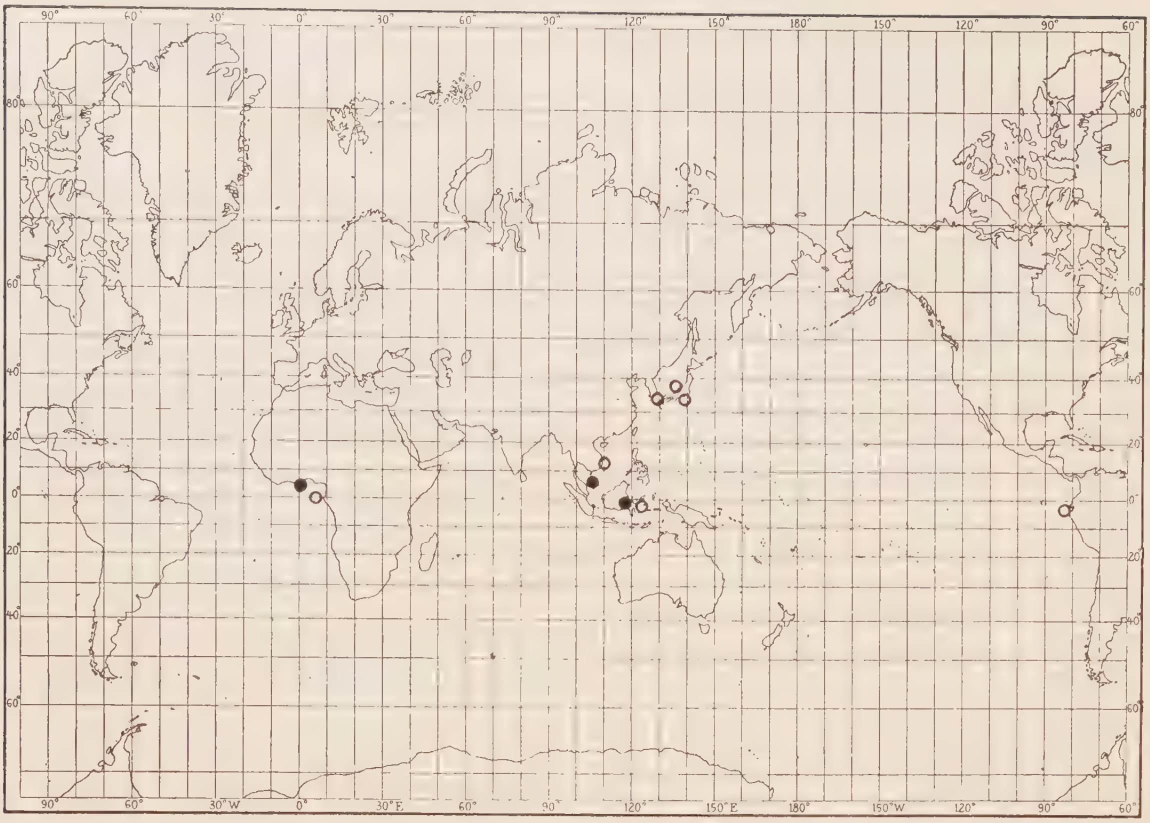


Fig. 12. Geographical distribution of *Stephanoscyphus corniformis*. ● Localities where the species was collected by the "Atlantide" and "Galathea" Expeditions. o Previous records.

The number of whorls in the specimens examined are as follows

"Galathea" stat. 451		"Atlantide" stat. 85	
length of tube, mm	no. of whorls	length of tube, mm	no. of whorls
14	3-4	10	6
16	5-8	11	5
22	7	12	8
24	7	14	5
		16	9

The soft tissues of the polyps are not in a suitable condition for anatomical description.

Further distribution of S. *corniformis* (see the map, textfig. 12).

The original specimens described by Komai were found near the coasts of Hondo, Japan, at depths of about 58-91 m. Some specimens mentioned in a letter from Sir Sidney Harmer to prof. Komai probably belong to this species; they were collected by the "Siboga" in the Malayan Archipelago east of Celebes, depth 75-94 m; Leloup has examined these specimens (1937 p. 61, fig. 30A) and referred them to *S. mirabilis* Allman. I am rather sure that the specimens recorded as *S. mirabilis* by Leloup (p. 62) from the following localities should likewise be referred to *S. corniformis:* Ilheos das Rolas in the Gulf of Guinea (fig. 38B), Machalillo off the coast of Ecuador in South America, depth 10 m (fig. 38C), and off Nhatrang in Viet Nam, depth 40 m (figs. 38D, E).

The species thus seems to have a circumglobal distribution in tropical seas in comparatively shallow water, 10-94 m.

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Explanation of Plate 1.

Figs. 1-2. Two specimens of *Stephanoscyphus simplex,* both from "Galathea" stat. 471 in the Sunda Trench, one without internal processes, the other with several whorls of processes.

Fig. 3. A specimen in strobilation, the tube containing several newly hatched medusae; stat. 436.

Fig. 4. Oblique section of the pedal disc; stat. 436.

Figs. 5-6. Two successive whorls of internal processes of one specimen, in which the theca has been cut open and spread out flat; stat. 299.

Figs. 7-11. Transverse sections of a specimen showing the soft tissues; stat. 436.

Fig. 7. Section of the pedicel; obs. the thick chitinous wall of the theca and the taenioles, two of which are broad, the two others very narrow.

Fig. 8. Section between two whorls of internal processes; obs. the circular outline of the four taenioles.

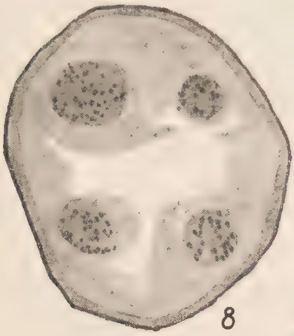
Fig. 9. Part of the same section in higher magnification.

Fig. 10. Section through a whorl of internal processes; obs. the more or less compressed taenioles.

Fig. 11. Part of the same section, showing one of the radial endodermal septa.

Figs. 12-13. *Stephanoscyphus corniformis.* Internal views of parts of thecae cut open and spread out flat to show the shape of the internal processes. Fig. 12 "Galathea" stat. 451, fig. 13 "Atlantide" stat. 85.

Figs. 1-3 are drawn by P. WINTHER, the others by the author.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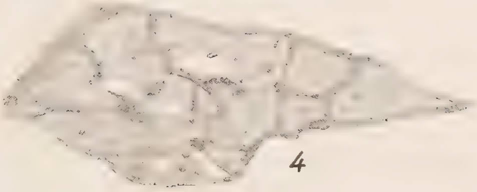
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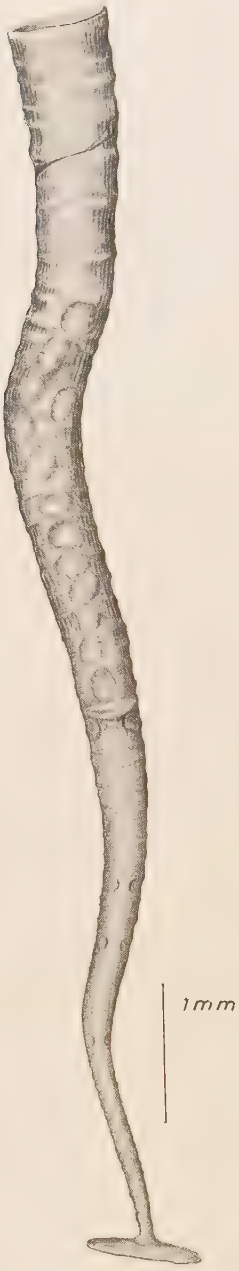
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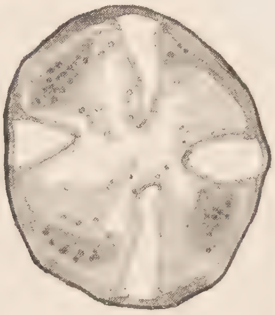
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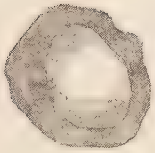
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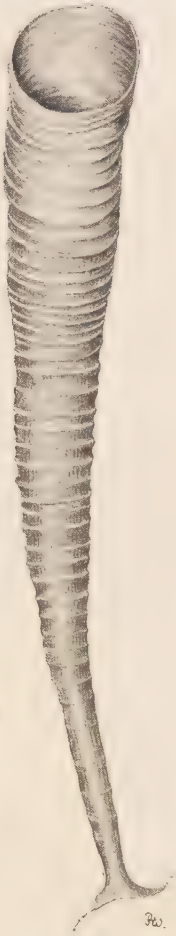
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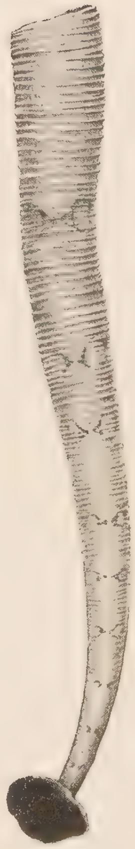
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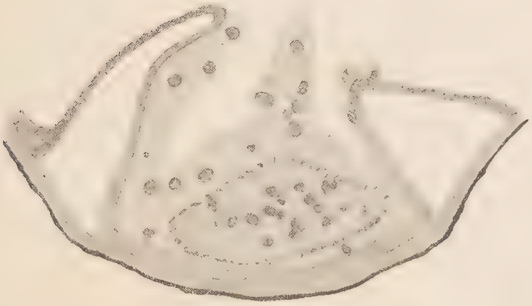
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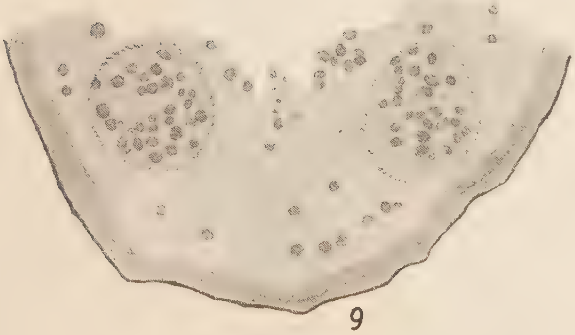
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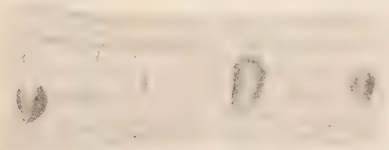
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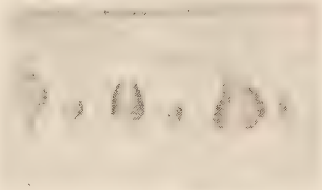
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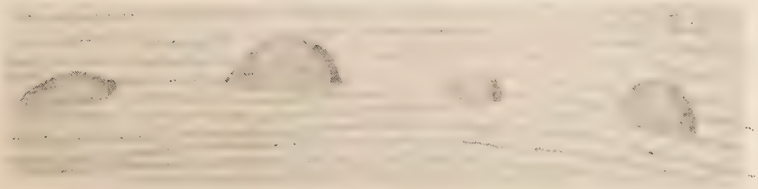
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15. 2. 59. 600. 125

ASCIDIACEA

By R. H. MILLAR
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A. INTRODUCTION

The Danish Deep-Sea Expedition in 1950, 1951 and 1952 collected ascidians from the Pacific Ocean, the Tasman Sea, Indonesian waters, the Indian Ocean and the Atlantic Ocean, in depths from 2084 to 7000 metres. This material makes an important contribution to our knowledge of the abyssal ascidian fauna and its geographical distribution.

All the material, including type specimens, is deposited in the University Zoological Museum, Copenhagen.

B. LIST OF STATIONS WITH SPECIES FOUND AT EACH

Station
30. *Bathystyeloides enderbyanus* (Michaelsen).
Molgula galatheae sp. n.
24. *Bathystyeloides enderbyanus* (Michaelsen).
52. *Bathystyeloides enderbyanus* (Michalesen).
Molgula galatheae sp. n.
66. *Bathystyeloides enderbyanus* (Michaelsen).
190. *Bathystyeloides enderbyanus* (Michaelsen).
196. *Styela milleri* Ritter.
217. *Culeolus suhmi* Herdman.
233. *Styela sericata* Herdman.
234. *Bathystyeloides enderbyanus* (Michaelsen).
Culeolus suhmi Herdman.
Styela sericata Herdman.
235. *Bathystyeloides enderbyanus* (Michaelsen).
238. *Bathystyeloides enderbyanus* (Michaelsen).
Styela sericata Herdman.
Culeolus suhmi Herdman.
280. *Hexacrobylus indicus* Oka.
Styela sericata Herdman.
Polycarpa albatrossi (Van Name).

Station
281. *Culeolus suhmi* Herdman.
282. *Polycarpa albatrossi* (Van Name).
Styela sericata Herdman.
Culeolus suhmi Herdman.
Hexacrobylus indicus Oka.
453. *Molgula immunda* (Van Name).
474. *Polycarpa albatrossi* (Van Name).
574. *Styela sericata* Herdman.
599. *Bathystyeloides enderbyanus* (Michaelsen).
601. *Cnemidocarpa bythia* (Herdman).
Styela sericata Herdman.
Bathystyeloides enderbyanus (Michaelsen).
602. *Cnemidocarpa bythia* (Herdman).
Styela sericata Herdman.
607. *Culeolus suhmi* Herdman.
651. *Cnemidocarpa bythia* (Herdman).
653. *Cnemidocarpa bythia* (Herdman).
654. *Abyssascidia wyvillii* Herdman.
Cnemidocarpa bythia (Herdman).
661. *? Culeolus suhmi* Herdman.

Station

663. *Distaplia galatheae* sp. n.
Styela sericata Herdman.
? Culeolus suhmi Herdman.
Molgula immunda (Hartmeyer) f. *monocarpa* n. f.

Station

664. *Styela sericata* Herdman.
665. *Dicarpa simplex* Millar.
668. *Octacnemus bythius* Herdman.
? Culeolus suhmi Herdman.
716. *Dicarpa simplex* Millar.

C. DESCRIPTION OF SPECIES

Family **CLAVELINIDAE**
Forbes and Hanley, 1848

Genus **Distaplia** Della Valle, 1881

Distaplia galatheae sp. n. (Fig. 1)

Material:

St. 663, 36°31'S. 178°38'W., Kermadec Trench, 24-2-1952, depth 4410 m. sandy clay; one specimen.

Diagnosis:

Test of a clear to somewhat milky appearance. Thorax at least as long as abdomen. Gonad beside intestinal loop. Larva with only one sensory pigment spot in cerebral vesicle.

Colony:

The single colony contains only three well-developed zooids. Test fairly firm, clear to milky in appearance, with the zooids showing through. The colony was attached by a broad base.

Zooid (Fig. 1A):

About 2.4 mm long. Thorax equal to or slightly larger than abdomen.

Siphons:

The oral siphon was not distinctly seen, but is apparently short. The atrial siphon is wider, conical or tubular and projecting dorsally, but the shape of the opening could not be seen in many zooids.

Oral tentacles:

The short finger-like tentacles probably number 12-16.

Branchial sac:

Four rows of stigmata with 3 quite prominent transverse bars between adjacent rows. No parastigmatic bars were seen. The dorsal languets, of which the second is larger than the first and third, are placed on the transverse bars a short distance down the left branchial wall.

Gut:

A long narrow and slightly curved oesophagus leads to the ovoid or almost globular stomach. No folds or markings could be seen on the wall of the stomach. The proximal chamber of the intestine is short and leads to the curved ascending limb.

Gonad:

A large ovoid body lying beside the intestinal loop and stomach represents the gonad, but separate ovary and testis could not be distinguished.

Brood pouch:

The brood pouch is about as large as the thorax, but does not extend beyond the posterior end of the abdomen. It is joined to the thorax by a short narrow stalk. In the zooids examined two embryos were present in each brood pouch.

Larva (Fig. 1B):

About 1.2 mm. long from the anterior end of the papillae to the base of the tail. In the best developed larvae there are three anterior papillae, of which two are dorsal and one is ventral. The papillae are quite like those of other species in the genus. Four rows of small stigmata are present in the branchial sac, and the gut is well differentiated. Both oral and atrial siphons are developed. The cerebral vesicle is, however, abnormal since it possesses only one pigmented sensory organ. It could not be determined with certainty whether this was the ocellus or the otolith, but its shape suggested an otolith. The tail,

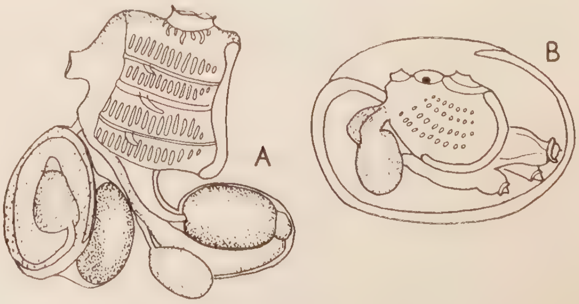


Fig. 1. *Distaplia galatheae* sp. n. A, zooid; B, larva.

when coiled round the larva, reaches the oral siphon.

Remarks:

No species of *Distaplia* has hitherto been found at great depths. The structure of the present species is little modified from that of species occurring in shallow waters. Only the larva, with its loss of one sensory organ from the cerebral vesicle, is modified and if the lost organ is in fact the ocellus, the modification is correlated with life in constant darkness.

Family **OCTACNEMIDAE** Herdman, 1888

Genus **Octacnemus** Moseley, 1876

Octacnemus bythius Moseley

(Figs. 2, 3; Plate 1, figs. 1, 2)

Octacnemus bythius Moseley, 1876, p. 287, pl. 44, figs. 7-13.

Material:

St. 668, 36°23′S. 177°41′E., Kermadec Trench, 29-2-1952, 2640 m, clay; one specimen.

External appearance:

The body is cylindrical to ovoid and about 1.7 cm. long. At its upper end it bears a crown of 8 flat triangular lobes, and at its lower end there is a roughened surface by which the animal was apparently attached during life. The greatest diameter across the lobes, when they are fully extended, is about 5.5 cm. The crown is not quite symmetrical as the 3 or 4 ventral lobes are longer than the others. A soft, transparent and rather thin test covers the whole surface, including the lobes. There is an opening in the test at the upper end of the body, on the area enclosed by the crown of lobes, and situated a little towards the dorsal side. This is the outer end of the oral opening. The triangular lobes are, as will be shown later, nothing more than the greatly developed lobes of the oral siphon surrounding the oral opening. The exhalent opening in the test could not be seen in this specimen but Moseley found it on the postero-dorsal surface, outside the crown of lobes. As the test is transparent the red-brown muscles of the lobes and body wall can be seen without dissection.

Internal structure:

In the fixed specimen there is a large cavity between the test and the upper, or internal, surface of the oral lobes and another surrounding the body and extending under the lobes. These two cavities have been wrongly called the oral or branchial cavity and the atrial cavity respectively, in several previous descriptions of *Octacnemus*. They may be artifacts and will be discussed later (see "Remarks"). The muscles of the body have already been carefully described in this and related species (Moseley, 1876; Herdman, 1888; Metcalf, 1900; Madsen, 1947). In the 'Galathea' specimen the muscles agree with existing accounts and are shown in fig. 2. On the oral lobes they consist of longitudinal muscles, which have generally been called radial muscles, and circular or transverse muscles. One longitudinal muscle lies between each two lobes and forks to send a branch along the margin of each adjacent lobe. The circular muscles are anatomically external to the longitudinal ones, lying on what has been called the aboral side of the lobes. Two rows of short stout muscles, one row on each side of the body, meet ventrally; these muscles appear to belong to the circular system. A few bands of muscle are also present on the dorsal side of the body, near the ganglion.

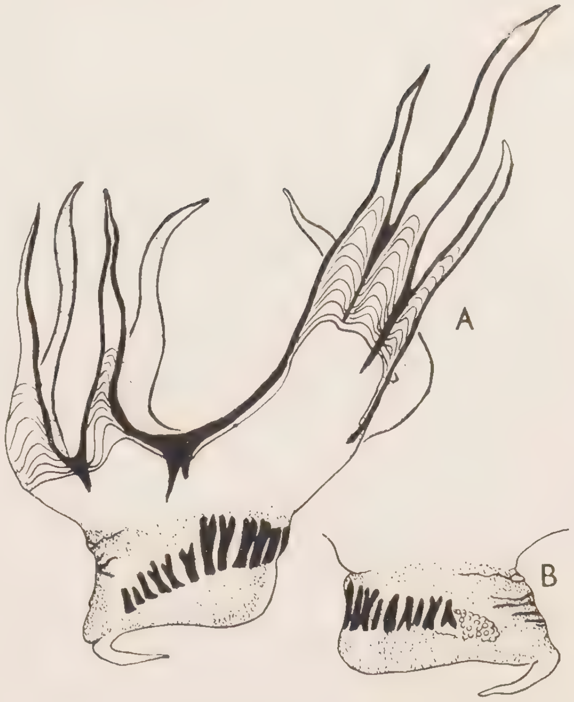


Fig. 2. *Octacnemus bythius* Moseley. A, animal removed from test; B, body from left. Muscles in black.

The ganglion is an ovoid white body which gives off a pair of large antero-lateral nerves, and a branched posterior nerve probably representing the paired posterior nerves and the median rapheal nerve. Immediately behind and slightly ventral to the ganglion is the globular neural gland, with a projecting funnel which has a simple opening. The

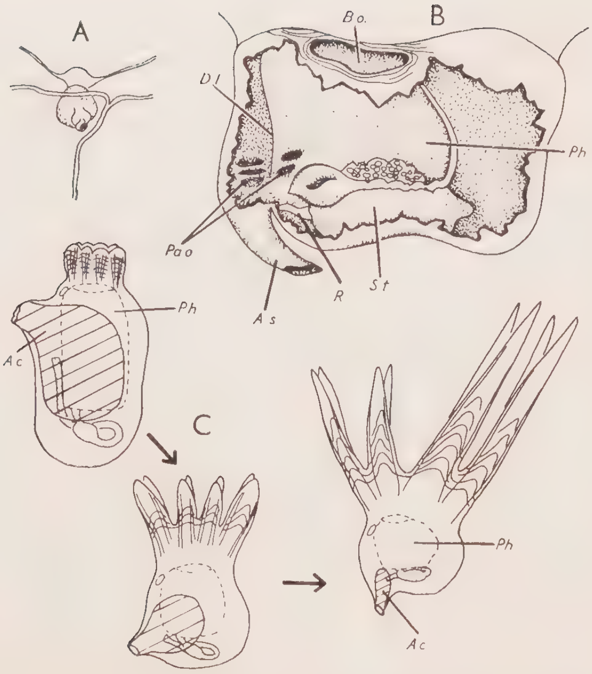


Fig. 3. *Octacnemus bythius* Moseley. A, ganglion and dorsal tubercle from ventral side; B, body from the right side, dissected, A. s., atrial siphon, B. o., branchial opening, D.l. dorsal line, P.a.o., pharyngo-atrial openings, Ph., pharynx, R., rectum, St, stomach; C, suggested evolution of *Octacnemus* from a simple enterogonid ascidian, A. c., atrial cavity.

external part of the oral opening, in the test, has been mentioned. The oral opening proper, which leads directly into the branchial sac, is moderately wide and is encircled by bands of muscle which are extensions of the mid-dorsal longitudinal muscle of the oral siphon. There is no trace of oral tentacles. The branchial sac is simple, its walls lacking stigmata, bars, and papillae. Ritter (1906), however, found a few vestigeal stigmata in his specimens of *O. herdmani,* a closely related, if distinct, species. There is a dorsal furrow representing the dorsal lamina of other ascidians, a wide endostyle, a retropharyngeal band and peripharyngeal bands encircling the oral opening. The pharyngo-atrial openings will be described later.

The oesophagus opens at the postero-dorsal corner of the branchial sac, but no details of the oesophagus, stomach or intestine were seen clearly. The rectum lies on the left of the stomach and opens into the atrial cavity.

Neither the atrial cavity nor the atrial siphon has been recognised in previous investigations of *Octacnemus.* The atrial cavity is a small pocket lying above and behind the postero-dorsal corner of the branchial sac and extending for a short distance in a ventral direction behind the sac. It is separated from the branchial sac by a thin partition which is perforated by two groups of pharyngo-atrial openings, one group on each side of the dorsal line. Each group of openings consists of two or three adjacent oval slits. I do not know whether these openings are transformed stigmata or newly acquired structures. The atrial siphon, as seen in the 'Galathea' specimen, is short and turned back to lie along the posterior side of the body, but this attitude was probably produced after death. I believe that the structure described and illustrated by Moseley (1876, pl. 44, fig. 10, r) as the rectum was in fact the atrial siphon of his specimen, as it corresponds exactly in position with the siphon in the 'Galathea' specimen. The end of the rectum lies within and at the base of the atrial siphon.

The ovary and testis, each a single compact mass, lie beside the stomach and intestine, but their detailed structure could not be seen, nor the nature of their ducts.

Remarks:

Since it was first described by Moseley *Octacnemus* has been studied by several workers, but its structure has never been satisfactorily related to that of other ascidians.

The very characteristic crown of lobes has not been previously recognised as the greatly developed oral siphon, the lobes themselves being the 8 enlarged oral lobes. The two surfaces of the crown of lobes have commonly been called the oral and aboral surfaces; these correspond to the internal and external surfaces of the oral siphon.

This interpretation, that the crown of lobes represents the oral siphon, is supported by (1) the position of the lobes surrounding the opening to the pharynx; (2) the arrangement of the muscles in longitudinal and circular systems with the circular system external; (3) the number of lobes corresponding to the number of oral lobes in the less modified simple ascidians like *Ciona* and *Ascidia;* (4) the arrangement of the lobes with a space between lobes occupying the mid-dorsal and mid-ventral positions, as in *Ciona;* and (5) the presence of test on both surfaces of the lobes, as it is on both external and internal surfaces of the oral siphon in other ascidians. The only important difference is the position of the longitudinal muscles which in *Octacnemus* lie between the lobes whereas in *Ciona* they are in line with the lobes. But this change only involves a redistribution of the constituent strands of the muscles. By accepting this view of the crown of lobes we see *Octacnemus* to be much less aberrant than has been thought.

The discovery of the atrial siphon and atrial cavity also brings *Octacnemus* into line with other ascidians. Hitherto the atrial cavity has either been thought to be absent or to be represented by the space between the test and the lower part of the body. Even without the discovery of the true atrial cavity the second interpretation would have been inadmissible since the space in question is bounded externally by the inner surface of the test and internally by the outer surface of the body wall. It is uncertain if this lower space and also the space above the lobes exist in the living animal or are artifacts as Ritter (1906) maintains, but I think that they are probably artifacts produced during fixation. As a living tissue the test must almost certainly maintain contact with the epidermis.

The peculiar structure of the branchial sac implies a method of feeding unlike that of most ascidians. It has been thought that *Octacnemus* is predatory since both Ritter (1906) and Madsen 1947) found the remains of relatively large animals in the gut. The 'Galathea' specimen also contains, in the upper test space, a large copepod of the species *Bradyidius armatus* Giesbrecht. I am indebted to Dr. W. Vervoort of the Zoological Laboratory, the University of Leiden, and also to Mr. R. V. Gotto of the Department of Zoology, The Queen's University, Belfast, for identifying this copepod. The copepod was probably forced out of the branchial sac and into the upper test space by contraction of the body during fixation. It seems likely that quite large animals form most of the food of *Octacnemus* rather than the diatoms, unicellular algae and other small organisms commonly eaten by ascidians. Perhaps, as has been suggested, the large muscular lobes play some part in capturing living animals. It may be, however, that only dead animals are taken, and Dr. Vervoort considers that the specimen of *B. armatus* found in the *Octacnemus* of the 'Galathea' collections may have been dead when engulfed. Whether or not *Octacnemus* captures animals in this way it certainly is not a filter feeder, as the branchial sac lacks stigmata and is therefore unable to strain small organisms out of a current of water. Indeed, it is probable that there is no constant current of water through the pharynx, and that the pharyngo-atrial openings serve only to allow the escape of water through the atrial siphon when the oral opening is closed and the body contracts. An intermittent current of water of this kind would be needed to remove faeces and the genital products.

With regard to the systematic position of *Octacnemus* several features, especially the unpaired gonads and the number of the oral lobes are characters found in the subclass Enterogona, and it is to this group that the genus should be assigned. The evolution of *Octacnemus* from an unspecialised enterogonid ascidian is suggested in fig. 3 C. The main changes involved are the great enlargement of the oral siphon, the simplification of the branchial sac and the reduction of the atrial cavity. These are all changes which are related to a changed method of feeding, the reduction of the atrial cavity probably having followed the loss of functional stigmata in the pharynx. In looking for a hypothetical ancestor of *Octacnemus* we must remember that although *O. bythius* and *O. herdmani* are solitary, there is one compound species, *O. patagoniensis* Metcalf. The genus may have derived from a primitive social enterogonid type with an organisation rather like that of *Perophora,* or from a solitary enterogonid type like *Ciona.*

Family **CORELLIDAE** Lahille, 1887

Genus **Abyssascidia** Herdman, 1880

Abyssascidia wyvillii Herdman. (Fig. 4)

Abyssascidia wyvillii Herdman, 1880, p. 470.

Material:

St. 654, 32°10'S. 175°54'W., Kermadec Trench, 18-2-1952, depth 5850-5900 m, pumice; two specimens.

External appearance:

The specimens measure 0.9 by 0.7 by 0.3 cm. and 1.0 by 0.7 by 0.2 cm. The body is somewhat compressed and smooth, being a little rougher only on the area of attachment.

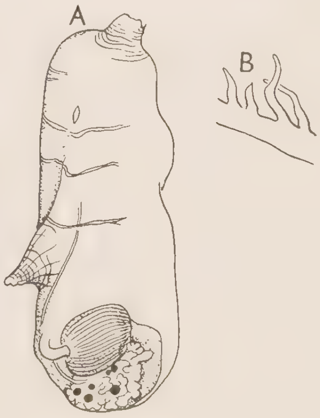


Fig. 4.
Abyssascidia wyvillii Herdman.
A, animal removed from test, from the right;
B, part of dorsal line with languets.

Test:

Cartilaginous and moderately thick; firm; semitransparent.

Body Wall:

Very thin. The muscles are few, widely separated and run round the body mainly in a dorsi-ventral direction.

Siphons:

The oral siphon is short but was not distinctly seen. Atrial siphon placed far back, about or a little posterior to the middle of the body; conical and indistinctly lobed.

Oral tentacles:

Not seen.

Dorsal tubercle:

Not seen.

Branchial sac:

The margin of the dorsal lamina bears a row of moderately long languets. Longitudinal bars are present but their number could not be determined, owing to the collapsed state of the branchial sac. About 3 oval stigmata occupy each mesh.

Gut:

The oesophagus is bent sharply downwards and leads to a wide ovoid or barrel-shaped stomach. Sixteen low narrow folds were counted on the exposed right wall of the stomach, and the concealed left wall may bear a similar number so that the stomach probably has altogether about 30 folds. HERDMAN (1882) gives the number as about 12, in the type specimen. The intestine makes a loop on the right of the posterior part of the branchial sac, passes dorsally on the left of the oesophagus and leads to the rectum which extends forward to the base of the atrial siphon.

Gonads:

A group of many closely crowded testis follicles occupies the right side of the intestinal loop. The ovary is represented by a few ova scattered amongst the testis follicles. The sperm duct passes to the left of the oesophagus and forward beside the rectum.

Remarks:

These two specimens from the Kermadec Trench agree very closely with the description by HERDMAN (1882) of the type specimen which was obtained by the "Challenger" Expedition south of Australia, at a depth of 4680 metres. Only in the number of folds on the stomach wall do they differ appreciably.

A. pediculata Sluiter which was collected by the "Siboga" Expedition between Australia and New Guinea, although rather similar, is distinguished by the possession of a stalk and by the arrangement of the gut.

Family **STYELIDAE** Sluiter, 1895

Genus **Cnemidocarpa** Huntsman, 1912

Cnemidocarpa bythia (Herdman) (Fig. 5)

Styela bythia Herdman, 1882, p. 63.

Material:

St. 601, 45°51'S. 164°32'E., Tasman Sea, 14-1-1952, depth 4400 m, Globigerina ooze; one specimen.

St. 602, 43°58'S. 165°24'E., Tasman Sea, 15-1 1952, depth 4510 m, bluish clay; three specimens.

St. 651, 32°10'S. 177°14'W., Kermadec Trench, 16-2-1952, depth 6960-7000 m, clay; three specimens.

St. 653, 32°09'S. 176°35'W., Kermadec Trench, 17-2-1952, depth 6180 m, pumice; four specimens.

St. 654, 32°10'S. 175°54'W., Kermadec Trench, 18-2-1952, depth 5850-5900 m, pumice; two specimens.

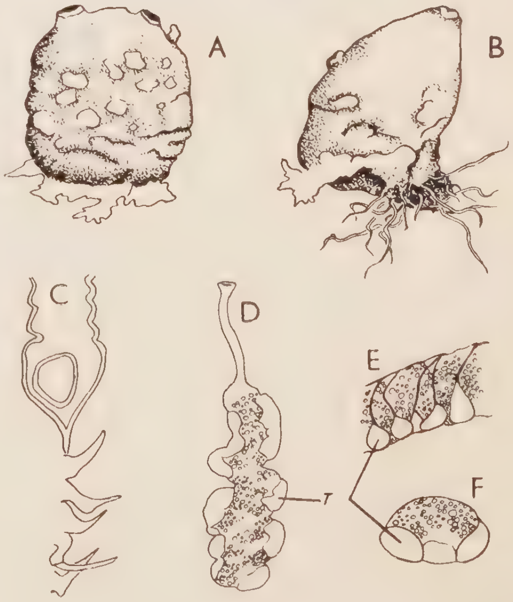


Fig. 5. *Cnemidocarpa bythia* (Herdman). A, a specimen without test hairs; B, a specimen with test hairs; C, dorsal tubercle and part of dorsal lamina; D, gonad; E, part of gonad to show arrangement of ovary and testis; F, transverse section of gonad. T., testis lobes.

External appearance:

The body is generally roughly rectangular in outline with the two siphons at the opposite corners of the upper edge. The surface is brown and rough, often coarsely wrinkled and in some specimens is provided with hair-like processes of the test near the basal area of attachment, although all specimens were fixed to hard objects.

Body wall:

Moderately thick, brown, and rather firmly adhering to the test. Longitudinal and circular muscles are quite strongly developed.

Dorsal tubercle:

A simple round, triangular or open horse-shoe shaped slit.

Branchial sac:

Herdman (1882) particularly noted that this species was distinguished by its dorsal lamina which has prominent teeth or languets. All of the specimens in the present collection which were examined showed this characteristic. The longitudinal bars of a specimen 7 mm. long were arranged thus:

dorsal lamina 1 (30) 7 (8) 3 (13) 7 (6) 3 endostyle.

Gut:

The gut lies far back in the body. About 10 longitudinal folds are present on the wall of the stomach. The pyloric caecum is curved, and swollen distally. The margin of the anus is almost plain.

Gonads:

On each side of the body there is one gonad, which varies from rather short to quite long and sinuous. The central part is occupied by the ovary and a number of rounded or pear-shaped testis follicles occupy the lateral and parietal parts of the gonad. The testis follicles are closely applied to the sides of the ovary, and give the gonads the form which distinguishes *Cnemidocarpa* from *Styela*. It has been suggested (Sluiter, 1914; Hartmeyer and Michaelsen, 1927; van Name, 1945) that this species is closely related, or perhaps identical, to *Styela tholiformis* Sluiter and *S. orbicularis* Sluiter, both from deep water. But these two species have gonads typical of the genus *Styela*, in which the testis follicles are distinctly separated from the ovary. Moreover the dorsal lamina of *S. tholiformis* and *S. orbicularis* has a plain undivided edge quite distinct from that of *C. bythia*.

Genus **Polycarpa** Heller, 1877

Polycarpa albatrossi (Van Name) (Fig. 6)

Pandocia albatrossi Van Name, 1912, p. 579, pl. 63, fig. 111, pl. 64, fig. 113, pl. 70, fig. 146; Hartmeyer, 1912, pp. 374, 378.

Polycarpa albatrossi Hartmeyer 1923, p. 223; Van Name 1954, pp. 256, 257; pl. 2, fig. 5; text fig. 155.

Material:

St. 280, 1°56′N. 77°05′E., Seychelles – Ceylon, 9-4-51, depth 4350 m, fine mud; one specimen.

St. 282, 5°32′N. 78°41′E., Seychelles – Ceylon, 11-4-1951, depth 4040 m, mud; 7 specimens.

St. 474, 9°49′S. 114°13′E., Sunda Trench, 11-9-1951, depth 3840-3810 m; one specimen.

External appearance:

The largest specimen is 9 mm. long; all are ovoid with the low siphons on the upper surface. Apart from the siphons and the area immediately round them the surface of the body is covered with long branched hairs each consisting of a short stout stem from the end of which arise several slender filaments. Foreign matter adheres to the hairs.

Oral tentacles:

There are about 32 slender oral tentacles.

Dorsal tubercle:

This is small with a rather simple opening which is slightly curved and either transverse or longitudinal.

Branchial sac:

These specimens have two or three low folds on each side of the branchial sac. Van Name (1945) describes two folds on each side, the remaining two being rudimentary or absent.

The longitudinal bars of one of the "Galathea" specimens were arranged thus: –

dorsal line 2 (12) 12 (8) 5 (3) 5 endostyle.

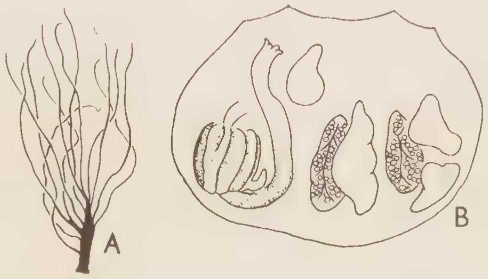


Fig. 6. *Polycarpa albatrossi* (Van Name). A, a test hair; B, left half of body showing gut, the two gonads, and four endocarps.

Gut:

The stomach has only about 12 folds, a small number compared with that recorded by Van Name (1912) who notes 20 to 25. A quite large gastric caecum is present. The intestine forms a simple loop lying close to the stomach. A number of shallow lobes surround the anus.

Gonads:

Most specimens have three gonads on the right and two on the left side. The gonads are of the usual type found in the genus. Van Name (1912, 1945) does not say how many gonads he found in the type specimens, stating only that they were "not very numerous".

Remarks:

In spite of slight differences in the branchial sac, stomach, and number of gonads, there is little reason to doubt that the present specimens represent *P. albatrossi*. The species has previously been recorded only from deep water in the western North Atlantic.

Genus **Styela** Fleming, 1882

Styela milleri Ritter (Fig. 7).

Styela milleri Ritter, 1906, p. 21; van Name 1945, p. 308, text-fig. 204.

Material:

St. 196, 29°55′S. 31°20′E., off Durban, 13/14-2-1951, depth 425-430 m, sandy mud and stones; one specimen.

External appearance:

The specimen is 7 mm. in greatest diameter, with a brown and somewhat wrinkled surface. On the upper side are the two openings, rather close together.

Body wall:

This is thin and of a purple-brown colour. The muscles consist of many fine longitudinal and circular strands.

Oral tentacles:

There are about 24 tentacles of alternating lengths.

Dorsal tubercle (Fig. 7A):

The rather small tubercle has a simple slightly curved longitudinal opening.

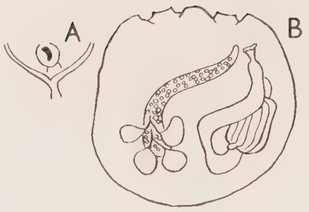


Fig. 7. *Styela milleri* Ritter. A, dorsal tubercle; B, gut and left gonad, from left.

Branchial sac:

The dorsal lamina is a moderately wide plain edged membrane. Four folds are present on each side. The folowing is the arrangement of longitudinal bars on the right side:

dorsal line 6 (11) 3 (9) 3 (7) 4 (5) 3 endostyle.

Only 2 stigmata are usually present between adjacent bars.

Gut (Fig. 7B):

The stomach has 21 complete longitudinal folds and a small pyloric caecum. There is a constriction near the end of the rectum, the terminal part of which widens. The anus has a lobed margin.

Gonads (Fig. 7B):

One gonad is present on each side, consisting of a long curved ovary with a few testis follicles gouped round its lower end.

Remarks:

In two respects the specimen from the "Galathea" collection differs slightly from Ritter's description of the type material. Firstly, the test lacks hairs, and secondly, the dorsal tubercle is simpler. But Van Name (1945) neither mentioned nor illustrated test hairs; and the smaller size of the present specimen may account for the simpler form of the dorsal tubercle. The differences do not therefore seem sufficient to distinguish the specimen from *S. milleri*.

Previous records of this species are from deep water off the west coasts of North and South America.

Styela sericata Herdman (Fig. 8)

Styela sericata Herdman, 1888, p. 153, pl. 11, figs. 14-16.

Cnemidocarpa platybranchia Millar, 1955, p. 226, fig. 3.

Material:

St. 233, 7°24′S. 48°24′E., Madagascar-Mombasa, 9-3-1951, depth 4730 m, Globigerina ooze; several specimens.

St. 234, 5°25′S. 47°09′E., Madagascar-Mombasa, 10-3-1951, depth 4820 m, Globigerina ooze; one specimen.

St. 238, 3°23′S. 44°04′E., off Kenya, 3980 m, Globigerina ooze; 5 specimens.

St. 280, 1°56′N. 77°05′E., Seychelles – Ceylon, 9-4-1951, depth 4350 m, fine mud; one specimen.

St. 282, 5°32′N. 78°41′E., Seychelles – Ceylon, 11-4-1951, depth, 4040 m, mud; 7 specimens.

St. 574, 39°45′S. 159°39′E., Tasman Sea, 18-12-1952, depth 4670 m; one specimen.

St. 601, 45°51′S. 164°32′E., Tasman Sea, 14-1-1952, depth 4400 m, Globigerina ooze; three specimens.

St. 602, 43°58′S. 165°24′E., Tasman Sea, 15-1-1952, depth 4510 m, bluish clay; one specimen.

St. 663, 36°31′S. 178°38′W., Kermadec Trench, 24-2-1952, depth 4410 m, sandy clay; four specimens.

St. 664, 36°34′S. 178°57′W., Kermadec Trench, 24-2-1952, depth 4540 m, clay; one specimen.

External apperance:

The largest specimen is 1.8 cm. in length. In all specimens the body is ovoid and more or less depressed.

The branched test hairs are generally most abundant on the sides of the body, less so on the ventral surface and usually few or absent on the dorsal surface. The oral siphon is terminal and the atrial siphon near the posterior end of the dorsal surface. Each siphon is short and indistincly lobed.

Oral tentacles:

In a small specimen these number about 16, and in the largest 36.

Dorsal tubercle:

Very small with a simple oval or crescentic slit.

Branchial sac:

In the largest specimen and in a few others the branchial wall is thrown into folds, but these may be artifacts produced by contraction, as they vary in number and distinctness. Several well preserved specimens show no trace of folds.

Gut:

In the specimens from the Swedish Deep-Sea Expedition (Millar, 1955) no pyrolic caecum was found, but the additional material from the 'Galathea' shows a small curved caecum.

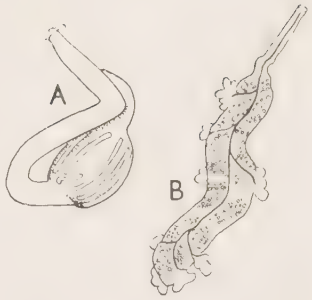


Fig. 8. *Styela sericata* Herdman.
A, gut; B, gonad.

Gonads:

The gonads are of variable length, slightly sinuous, and are intermediate between the *Styela*-type and the *Cnemidocarpa*-type.

Remarks:

After examining the more abundant material from the present collection I have decided that the three specimens from the Swedish Deep-Sea Expedition on which I based the species *Cnemidocarpa platybranchia* (Millar, 1955) do in fact represent *S. sericata* Herdman. Herdman's description is not very detailed, but the shape of the body, the distribution of the test hairs, the branchial sac, and the number of gonads agree with the 'Galathea' specimens.

Genus **Bathystyeloides** Seeliger, 1905

Bathystyeloides enderbyanus (Michaelsen) (Fig. 9)

Bathyoncus enderbyanus Michaelsen, 1904, p. 226. pl. 10, fig. 1., pl. 13, figs. 45-48.

Bathystyeloides atlantica Millar, 1955, p. 229, fig. 5.

Material:

St. 24, 3°54′N. 8°22′W., Monrovia-Takoradi, 15-11-1950, depth 3200 m, mud; one specimen.

St. 30, 0°42′N. 5°59′W., Monrovia-Takoradi, 18-11-1950, depth 5160 m, mud; many specimens.

St. 52, 1°42′N. 7°51′E., San Thomé-Camaroon, 30-11-1950, depth 2550 m, muddy clay; one specimen.

St. 66, 4°00′S. 8°25′E., 5-12-1950, depth 4020 m, mud; 6 specimens.

St. 190, 29°42′S. 33°19′E., off Durban, 3-2-1951, depth 2760 m, Globigerina ooze; one specimen.

St. 234, 5°25′S. 47°09′E., Madagascar-Mombasa, 10-3-1951, depth 4800 m, Globigerina ooze; one specimen.

St. 235, 4°47′S. 46°19′E,, north of Madagascar, 11-3-1951, depth 4810 m, Globigerina ooze; 3 specimens.

St. 238, 3°23′S. 44°04′E., off Kenya, 13-3-1951, depth 3980 m, Globigerina ooze; 6 specimens.

St. 599, 45°47′S. 164°39′E., Tasman Sea, 13-1-1952, depth 4390 m; one specimen.

St. 601, 45°51′S. 164°32′E., Tasman Sea, 14-1-1952, depth 4400 m, Globigerina ooze; one specimen.

External appearance:

The specimens range in length from 6 mm. to 18 mm. The dorsal surface is fairly free of test hairs, but on the ventral surface and especially on a belt round the sides of the body there are many hairs. Most of these hairs are branched, having a short stout common stem from the end of which arise a number of fine tapering filaments.

Body wall:

A single large endocarp is present on each side.

Dorsal tubercle:

The opening is small and simple, in shape either a longitudinal oval slit or a transverse crescentic slit.

Branchial sac.:

In a specimen 16 mm. long there were about 135 longitudinal bars on each side of the branchial sac, but a specimen of length 12 mm. had only about 75 on each side.

Gut:

At least 12 folds on the wall of the stomach.

Gonads:

One on each side, straight or gently curved. Most of each gonad is occupied by the ovary. The testis follicles vary in their arrangement, being in some specimens regularly distributed along each side of the ovary, and in others grouped into large irregularly placed masses. The oviduct and common sperm duct are short and separate from each other.

Remarks:

The type specimen described by Michaelsen (1904) was from 4636 m in the Antarctic Ocean. A second specimen was collected by the Swedish Deep Sea Expedition, in the Atlantic Ocean, at a depth of 5250-5300 m, and was described by me (Millar, 1955) as a new species *B. atlantica*. The diagnostic characters which I used to separate this species from *B. enderbyanus* were (1) the presence of test-hairs, (2) over 100 longitudinal bars on each branchial wall, (3) the even distribution of testis follicles round the ovary. In my account of *B. atlantica* I suggested that the type specimen of *B. enderbyanus* did in fact possess test-hairs which Michaelsen interpreted as filamentous algae, and that the separation of the two species may rest mainly on the number of longitudinal bars in the branchial sac and the distribution of the testis follicles.

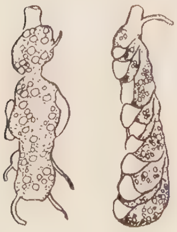


Fig. 9. *Bathystyeloides enderbyanus* (Michaelsen). Gonad.

The new and more plentiful material from the 'Galathea' provides, in both the gonads and the branchial sac, conditions intermedlate between the two species. The separation of *B. atlantica* can no longer be maintained, and that name becomes a synonym of *B. enderbyanus*.

This species is apparently very widely distributed, having been recorded from the equatorial Atlantic Ocean, the western Indian Ocean, the Tasman Sea, and the Antarctic.

Genus **Dicarpa** Millar, 1955

Dicarpa simplex Millar (Fig. 10; Pl. 1, fig. 3)

Dicarpa simplex Millar, 1955, p. 225, fig. 2.

Material:

St. 665, 36°38′S. 178°21′W., Kermadec Trench, 25-2-1952, depth 2470 m, clay; many specimens.

St. 716, 9°23′N. 89°32′W., Acapulco-Panama, 6-5-1951, depth 3570 m, clay; 8 specimens.

External appearance:

The specimens in this collection are indistinguishable from those collected by the Swedish Deep-Sea Expedition, from which the type description was made.

Gut:

It is now possible to add detail to the incomplete description previously given (Millar, 1955). The oesophagus is a wide vertical slightly curved tube, leading down to the posterior end of the stomach. The stomach itself lies almost vertically, behind the branchial sac, and has 6 to 8 longitudinal folds on its wall. These folds are mainly developed on the right side of the stomach, the left side, which is adjacent to the intestine, being flat. The intestine leaves the lower anterior end of the stomach and

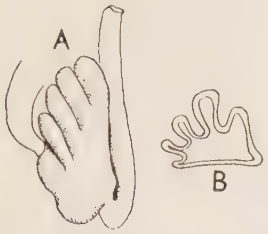


Fig. 10. *Dicarpa simplex* Millar. A, gut; B, transverse section of stomach.

bends upwards almost immediately to ascend vertically on the left of the stomach.

Gonads:

Most specimens examined showed the characteristic arrangement, with one polycarp-type gonad on each side of the body, but in one animal there were one small and two large gonads on one side, and one on the other side.

Remarks:

The only previous record of this species is from 4540-4600 metres in the north Atlantic Ocean. It is remarkable that it should also occur in the Kermadec area of the south Pacific Ocean.

The genus *Dicarpa* is obviously derived from the *Polycarpa* stock, as evidenced by the type of gonads. Specialization has taken the form of a reduced number of gonads and simplification in the branchial sac. These two characters are probably related to the very restricted space available in the small body.

Family **PYURIDAE** Hartmeyer, 1908

Genus **Culeolus** Herdman, 1881

Culeolus suhmi Herdman (Fig. 11)

Culeolus suhmi Herdman, 1882, p. 86.

Material:

St. 217, 14°20′S. 45°09′E., Mozambique Channel, 27-2-1951, 3390 m; two specimens.

St. 234, 5°25′S. 47°09′E., Madagascar-Mombasa, 10-3-1951, 4820 m, Globigerina ooze; many specimens.

St. 238, 3°23′S. 44°04′E., off Kenya, 13-3-1951, depth 3980 m; several specimens.

St. 281, 3°38′N. 78°15′E., SW of Ceylon, 10-4-1951, 3310 m, Globigerina ooze; one specimen.

St. 282, 5°32′N. 78°41′E., Seychelles - Ceylon, 11-4-1951, depth 4040 m, mud; several specimens.

St. 607, 44°18′S. 166°46′E., Tasman Sea, 17-1-1952, depth 3830 m; one specimen.

External appearance:

The proportions of body and stalk vary; one typical specimen has a body length of 2.5 cm. and a stalk length of 12.0 cm. The ventral edge of the body is nearly straight and the dorsal and posterior edges arched. Oral siphon projecting as a short tube; atrial opening moderately large and not projecting. An oblique line of prominent finger-like papillae completely encircles the atrial or posterior end of the body. The stalk is slender and marked with an irregular network of internal trabeculae.

Test:

The surface of the test is raised into small low rounded swellings, many of which have a short central papilla.

Oral tentacles:

Large and simply branched.

Dorsal tubercle:

The opening of the dorsal tubercle is of variable shape and in three specimens examined from Station 234 was a narrow longitudinal slit either curved to the right or left, or very slightly S-shaped and transverse. In the specimen from Station 607 the opening was horse-shoe-shaped, facing forwards.

Branchial sac:

The folds usually bear 10-14 longitudinal bars.

Gonads:

Two gonads are present on each side of the body, the ventral one on the left lying within the intestinal loop. The ovary is continuous along the whole length of the gonad, and is also enlarged at intervals to produce a number of rounded swellings. It is on these swellings alone that the testis is developed, forming a mass of follicles covering the dorsal side. Each gonad has a single short oviduct and sperm duct.

Remarks:

Culeolus is a very distinct deep water genus, but its subdivision into species is unsatisfactory as already noted by Van Name, (1945).

These specimens described above were taken from great depths in the Indian Ocean and Tasman Sea. They bear such a close resemblance to the original description of *C. suhmi,* given by Herdman (1882) and the later description by Van Name (1945) that, although *C. suhmi* has hitherto

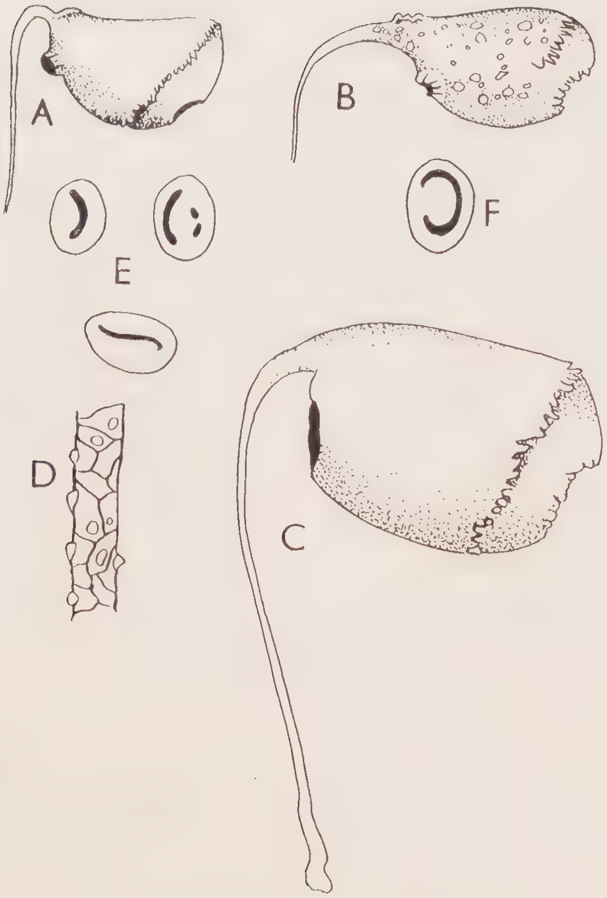


Fig. 11. *Culeolus suhmi* Herdman. A, specimen from St. 234; B, specimen from St. 668; C, specimen from St. 661; D, part of stalk; E, dorsal tubercles of specimens from St. 234; F, dorsal tubercle of specimen from St. 668.

been recorded only from the Atlantic Ocean, I cannot doubt that we are dealing with the same species.

Specimens of this genus are also in the collection from:

(1) St. 661, 36°07′S. 178°32′W., Kermadec Trench, 23-2-1952, 5340-5230 m; one specimen.

(2) St. 663, 36°31′S. 178°38′W, Kermadec Trench, 24-2-1952, 4410 m; one specimen.

(3) St. 668, 36°23′S. 177°41′E., Kermadec Trench, 29-2-1952, 2640 m, clay; 4 specimens.

The material from Stations 663 and 668 appears to represent one species, but I am undecided whether it is *C. suhmi*. The most striking difference is that the fringe of finger-like papillae round the posterior end is incomplete, being absent from the dorsal part of the body. The stalk bends at a less acute angle on leaving the body than is usual in *C. suhmi*, and the stalk is longer and thinner. As far as I can judge the internal structure does not differ significantly. Since the range of variation in *C. suhmi* has never been defined, and the features distinguishing the specimens from the Kermadec Trench are all external ones, I am inclined to include those specimens also in *C. suhmi*, at least provisionally. But I should be prepared to remove them if further specimens showed the same constant characters.

The single specimen from Station 661, also in the Kermadec Trench, has the body 5.5 cm. long and stalk 7.5 cm. long. As there is a complete circle of finger-like papillae round the posterior end of the body, this specimen might be regarded as a large example of *C. suhmi*, but the stalk is relatively much shorter than in most of the specimens of that species. *C. murrayi* Herdman approaches this specimen in proportions and in the presence of a complete fringe of papillae, but according to HERDMAN (1882) *C. murrayi* has one gonad on each side. *C. gigas* Sluiter has similar proportions but it also has a single gonad on each side and it is possible that *C. murrayi* and *C. gigas* may be synonymous. I am inclined to include this specimen in *C. suhmi*, in spite of the apparent differences, at least until the whole genus can be reviewed. This solution is not entirely satisfactory because a review of the genus must depend on an examination of much more material, from different areas, and the difficulties of getting many specimens from very great depths are such that an opportunity for a complete survey of the genus may not occur for a long time.

Family **MOLGULIDAE** Lacaze-Duthiers, 1887

Genus **Molgula** Forbes and Hanley, 1848

Molgula immunda (Hartmeyer)

Caesira immunda Hartmeyer, 1909-1911, p. 1324.

Material:

St. 453, 3°56′S. 118°26′E., Macassar Strait, 24-8-1951, depth 2000 m, clay; one specimen.

External appearance:

The specimen is about 2 cm. in diameter, very soft and almost transparent, of a round outline and perhaps slightly flattened laterally.

Test:

Soft and clear, with short tag-like hairs scattered over the surface. In dissection the test separates into an outer tougher layer and an inner softer layer.

Siphons:

The siphons are quite widely separated. The oral siphon is short and conical, the atrial siphon long and gradually tapering.

Dorsal tubercle:

The opening is small, narrow and longitudinal.

Branchial sac:

The 7 folds on each side are tall, each with up to 20 longitudinal bars. In this specimen the infundibula are tall, narrow and finger-like, rising far into the folds. Van Name (1945) describes the infundibula as "rather low".

Gut:

The gut is confined to the postero-ventral part of the body, forming a rather open vertical S-shaped loop.

Gonads:

The position and structure of the gonads are characteristic of this species. On the left side a gonad lies within the primary loop of the gut which it almost completely fills. On the right is a similar gonad. Each gonad is almost circular in outline with a central ovary and radially arranged testis follicles which are pear-shaped and somewhat lobed or sub-divided.

M. immunda f. **monocarpa** n.f. (Fig. 12).

Material:

St. 663, 36°31'S. 178°38'W., Kermadec Deep, 24-2-1952, depth 4410 m, sandy clay; 2 specimens.

Diagnosis of form:

As species but with one gonad on the right side and none on the left.

External appearance:

Body ovoid and slightly depressed, covered with rather short test hairs which are most numerous on the lateral and ventral surfaces. Siphons not at all, or scarcely, visible externally.

Test:

Rather thin and flexible.

Body wall:

Thin and semi-transparent. The muscles, which are distinct but not specially strong, are best developed on the dorsal part of the body. They consist of longitudinal and circular muscles, both sets originating from the siphons.

Siphons:

The internal siphons are distinct but short, the oral siphon with 6 pointed lobes and the atrial siphon with 4 pointed lobes. On the oral siphon the three dorsal lobes are much longer than the ventral ones.

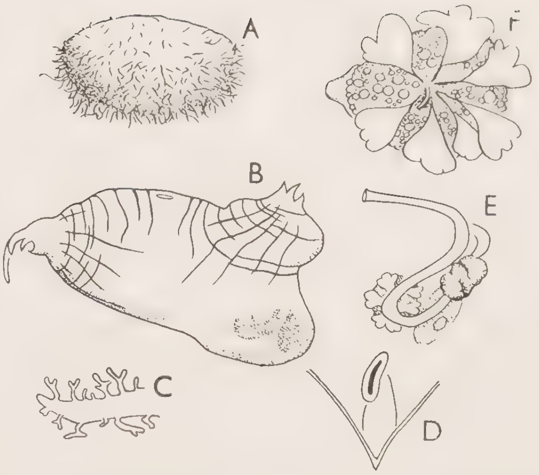


Fig. 12. *Molgula immunda* f. *monocarpa* n. f. A, intact animal; B, animal removed from test; C, part of a tentacle; D, dorsal tubercle; E, gut, with renal sac and gonad of right side; F, gonad.

Oral tentacles:

About 12 tentacles, compound but not strongly branched.

Dorsal tubercle:

A simple slightly curved longitudinal slit.

Branchial sac:

The dorsal lamina is moderately long and increases in width towards the posterior end. Its margin is plain. In one specimen 8 tall folds were present on the left side; only 6 could be seen on the right side but there may have been more. The exact number of folds could not be determined in the other specimen, but there were about 7 on each side. The folds are peculiar as each seems to consist of up to 10 longitudinal bars but no stigmata, which are confined to the flat portion of the branchial wall, and arranged in double spirals.

Gut:

The gut is confined to the posterior part of the left side of the body. The short curved oesophagus leads into a rather small barrel-shaped stomach, and the intestine makes an S-shaped bend. The rectum is straight and moderately long.

Gonad:

The single gonad is on the right side. It consists of a central ovoid to circular ovary, and 4 to 7 pear-shaped lobed testis follicles radially arranged on the mesial surface of the ovary. Individual sperm ducts converge to a central point from which arises a short slender common sperm duct. The oviduct is very short and inconspicuous.

Renal vesicle:

The renal vesicle lies far back on the right side, immediately posterior to the gonad. It is sausage-shaped and contains a large concretion.

Remarks:

I have given a full account of this form because further specimens might prove it to be specifically distinct from *M. immunda*. The only important difference that I find is the absence of a gonad on the left side. This is a feature which might have arisen within the species on account of the restricted space available for a gonad within the small primary loop of the intestine. As only two specimens are present in the collection I am not able to decide whether they represent a local variation or a separate species, but it seems best to regard them as a form of *M. immunda*.

Molgula galatheae sp. n. (Fig. 13)

Material:

St. 30, 0°42′N. 5°59′W., Monrovia – Takoradi, 18-11-1950, depth 5160 m, mud; one specimen.

St. 52, 1°42′N. 7°51′E., San Thomé – Camaroon, 30-11-1950, depth 2550 m, muddy clay; several specimens.

Diagnosis of species:

Test soft, with very fine hair-like processes. Circular and longitudinal muscles thin and regular. Siphons toothed. Oral tentacles large and tri-pinnate. Dorsal tubercle with longitudinal slit. Dorsal lamina with plain edge. Branchial sac with 5 tall narrow folds on each side, each fold with one longitudinal bar. Tall transverse bars. Stigmata spiral, crossed by numerous radial vessels on each of which is a row of papillae. Gut confined to posterior end of body. One gonad on each side, each consisting of a mass of testis follilcles half enclosing an ovoid ovary. Renal sac postero-ventral to right gonad.

External appearance:

The specimens from St. 52 form a mat owing to the interlacing of their test hairs. The largest specimen is 2.0 cm. in greatest diameter. All have an ovoid form obscured by a thick coat of test hairs.

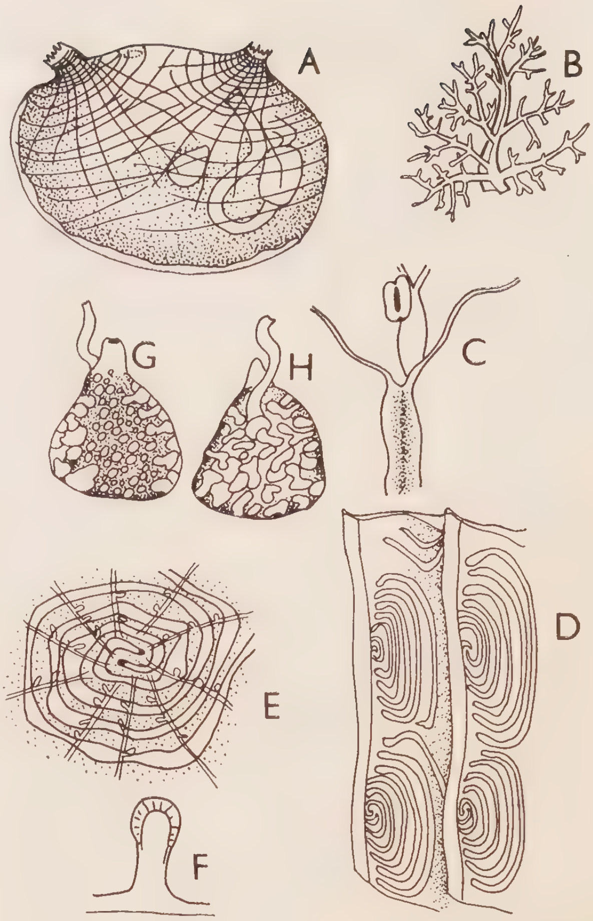


Fig. 13. *Molgula galatheae* sp. n. A, animal removed from test; B, oral tentacle; C, dorsal tubercle and part of dorsal lamina; D, part of branchial wall; E, stigma; F, branchial papilla; G, parietal aspect, and H, mesial aspect, of gonad.

Test:

This is soft and flexible, and almost completely covered with very fine processes to which are attached the shells of Foraminifera.

Body wall:

The body wall is thin. Its muscles consist of regular slender circular and longitudinal strands.

Siphons:

The siphons are short and conical, with toothed margins.

Tentacles (Fig. 13B):

There are 8 large oral tentacles and about the same number of smaller ones alternating with these. The largest tentacles are tri-pinnate.

Dorsal tubercle (Fig. 13C):

All specimens examined had a similar tubercle, which is small with a narrow longitudinal slit-like opening.

Branchial sac:

The dorsal lamina is a wide raised band with two low plain-edged membranes instead of one. Five narrow folds are present on each side of the branchial sac and each fold bears on its summit one tall longitudinal bar (Fig. 13D). There are no bars between folds. Below each fold is a row of spiral stigmata. Each stigma is long and regularly coiled (Fig. 13E). A series of up to 10 radial vessels crosses each stigma and these vessels bear papillae, which are short and finger-shaped with a slightly swollen end. No cilia were seen on the papillae but the preservation may not have been sufficiently good to show them, as very few can be seen on the stigmata themselves. Transverse bars are also present connecting adjacent folds and with the folds form a series of deep pockets on the branchial walls.

Gut:

This is confined to the posterior part of the body. The oesophagus is bent before joining the stomach, which is ovoid with wide longitudinal folds. The intestine and rectum are of uniform diameter. The intestinal loop is almost closed. The margin of the anus is plain.

Gonads (Fig. 13G, H):

One gonad is present on each side of the body. On the left side it is generally a short distance anterior to the intestinal loop but in some specimens it overlaps the intestine and occasionally appears to lie partly within the loop. The right gonad has a corresponding position on the right body wall. In most specimens the gonad is pear-shaped or almost globular. The central and parietal parts are occupied by the ovoid ovary ending in a short oviduct. The pear-shaped and lobed testis follicles form a compact mass on the mesial surface of the ovary and spread also round its lateral parts. The sperm duct arises from the mesial side of the gonad, at its narrow end, and projects freely. It is longer than the oviduct.

Renal sac:

The slightly curved renal sac lies on the right side of the body a short distance from the gonad and postero-ventral to it.

Remarks:

This species is distinguished from others in the family Molgulidae particularly by the nature of the branchial folds and by the presence of papillae on the radial vessels of the stigmata.

The papillae of the radial vessels are not homologous with the branchial papillae of the Phlebobranchiata, which are present on the longitudinal bars. In *Molgula galatheae* the papillae are new structures whose function is not known. They may serve to hold the mucous sheet from the surface of the stigmata but I do not know what might be the significance of this device in the process of feeding.

Family **HEXACROBYLIDAE** Seeliger, 1906

Genus **Hexacrobylus** Sluiter, 1905

Hexacrobylus indicus Oka (Fig. 14)

Hexacrobylus indicus Oka 1913, p. 6, fig. 4.

Hexacrobylus arcticus Hartmeyer 1923-24, p. 133, pl. 1, figs. 5, 6.

Material:

St. 280, 1°56′N. 77°05′E., Seychelles – Ceylon, 9-4-1951, depth 4350 m, fine mud; two specimens.

St. 282, 5°32′N. 78°41′E., Seychelles – Ceylon, 11-4-1951, depth 4040 m, mud; two specimens.

External appearance:

The body is ovoid and the largest of the specimens is 1.5 cm. long. In their shape, coating of test hairs, and nature of oral and atrial siphons the new specimens agree closely with Oka's type specimens. The most striking external feature is the group of six large lobes surrounding the oral siphon, two dorsal and four ventral. Each of these lobes is shaped like a hand with the fingers spread and curved.

Siphons:

When the test is removed the body wall of the oral siphon is seen to correspond in shape to the external appearance of the siphon. A strong circular muscle runs round the rim of the oral siphon immediately behind the lobes and each lobe has a longitudinal muscle passing along its internal face. The function of these muscles will be referred to later. The oral siphon is lined with test, the conspicuous sac-like lining of the siphon being left with the general test when the body is removed.

The atrial siphon is long and bent upwards. Its opening has no prominent lobes.

Body Wall:

The body wall is thin and transparent and has a sparse coating of small tag-like projections evidently

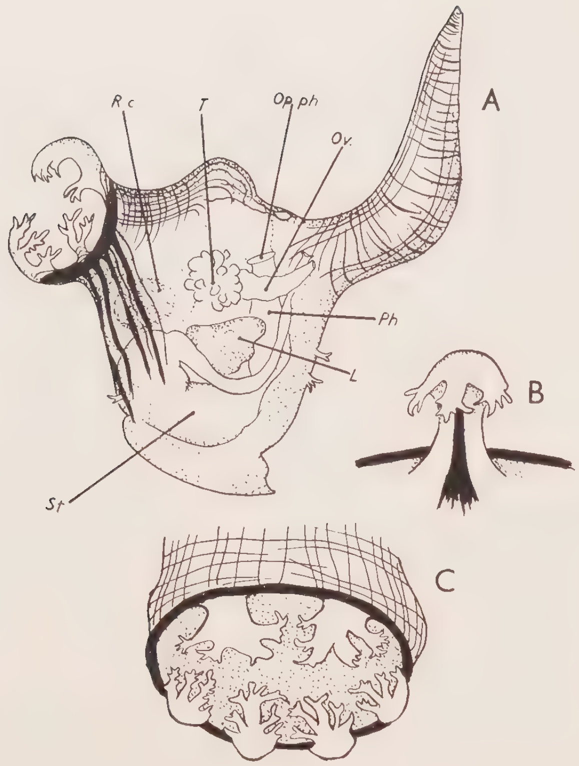


Fig. 14. *Hexacrobylus indicus* Oka. A, animal removed from test, from left side; B, one of the oral lobes seen from the opening of the siphon; C, end of the oral siphon. L, lobe of liver, Op.ph., opening to pharynx at base of oral siphon, Ov., ovary, Ph., pharynx, R.c., renal concretion, St., stomach, T., testis.

corresponding to the short hairs of the test. Slender circular muscles are present on each siphon. The longitudinal muscles of the oral siphon are divided into a ventral set of strong bands passing down towards the lower end of the body, and a dorsal set of finer strands reaching only to the base of the oral siphon. Longitudinal muscle strands are also present on the atrial siphon.

The internal organs correspond closely with Oka's description. The atrial cavity is comparatively small and extends from the base of the atrial siphon as a short pouch on each side of the pharynx.

Remarks:

The most interesting features of the species are the reduction of the pharynx with the complete elimination of stigmata, and the large size and complexity of the oral siphon. The two conditions are related, both being concerned with feeding habits. Examination of the stomach and intestine of two specimens in the 'Galathea' material shows that small swimming crustaceans, mainly copepods, are taken in, and these probably form a large part of the food of the species. The modified pharynx is of course unable to produce a water current or to filter out small organisms. Instead it seems likely that larger animals are captured individually by means of the oral siphon and passed by muscular action of the siphon back into the pharynx. It is not known whether the crustaceans are captured alive or whether they are already dead when taken in, having died and sunk to the bottom.

The oral siphon is adapted for the capture of comparatively large single organisms, by its large size, its greatly developed hand-like lobes, and its powerful muscles. The longitudinal muscles which lie on the internal face of the oral lobes are well placed to draw the lobes quickly across the opening of the siphon, which the terminal sphincter muscle also closes.

In addition to these anatomical adaptations there are probably also physiological adaptations to this method of feeding. In normal filter-feeding ascidians, for instance, a large and possibly active animal within the oral siphon would elicit the ejection reflex by which the stimulated siphon opens to allow the expulsion of the organism causing the stimulation. In *Hexacrobylus* this reflex might prevent feeding and may have been eliminated.

Hexacrobylus and the comparatively unrelated *Octacnemus* show remarkable convergence in the modified oral siphon and pharynx, both concerned with the change from filter-feeding to the intake of large single animals.

Three species have been described in this genus: *H. psammatodes* Sluiter from near the Celebes, *H. indicus* Oka from near Ceylon, and *H. arcticus* Hartmeyer from the North Atlantic Ocean. *H. psammatodes* differs from the other two species in a number of ways. *H. indicus* and *H. arcticus,* however, have much in common, and it has always been doubtful if they are distinct. When HARTMEYER (1923-24) established *H. arcticus* he admitted the difficulty of finding characters which clearly separated it from *H. indicus,* but he distinguished *H. arcticus* by (1) its smaller size, (2) the position of its siphons, and (3) the equal size and greater subdivision of the oral lobes.

Through the courtesy of the University Zoological Museum, Copenhagen, I have been able to examine six specimens from the original material collected by the 'Ingolf' Expedition, on which the species *H. arcticus* was based. The smaller size of the specimens taken by the 'Ingolf' is in itself not a good character, as the size may depend largely on the local environment. Moreover the specimens taken by the 'Galathea' are intermediate in size between Oka's specimens of *H. indicus* and Hartmeyer's specimens of *H. arcticus*. The position of the siphons is not greatly different, but the atrial siphon of *H. arcticus* is shorter and straighter than that of *H. indicus*. I consider this also an insufficient character for separating the species. There is no important difference in the structure of the oral siphon, although *H. indicus* has the two dorsal lobes enlarged whereas *H. arcticus* has six equal lobes as Hartmeyer remarked.

An examination of the new material collected by the 'Galathea' and a re-examination of the original material from the 'Ingolf' collections have convinced me that the similarities between *H. arcticus* and *H. indicus* are more important than the differences, and I therefore regard *H. arcticus* as a synonym of *H. indicus*.

D. DISCUSSION

The material in this collection establishes the presence of ascidians down to a depth of 7000 metres, and it is reasonable to suppose that they penetrate to the extreme depths of the ocean.

Of the species collected, six *(Polycarpa albatrossi, Styela sericata, Bathystyeloides enderbyanus, Dicarpa simplex, Culeolus suhmi* and *Hexacrobylus indicus)* are already known from areas geographically remote from those in which they were collected by the 'Galathea'. This is further evidence of the wide geographical distribution of species inhabiting very deep water. (See figs. 15-20).

The difficulties of collecting material from the abyssal region make it unlikely that many specimens would be taken in a single haul, and the number of individuals, for example of *Culeolus suhmi* at Station 234, probably represents a density of population comparable with that of shallow-water species.

Although moderately dense populations may occur, few species have succeeded in penetrating to great depths and these few species have been modified by the conditions of life there. The adaptive modifications are mainly of external form. Two common modifications are the possession of a stalk, and the development of filamentous processes on the test. Only those forms that live attached to a solid object lack one or other of these adaptations. Thus *Distaplia galatheae, Abyssascidia wyvillii,* and *Cnemidocarpa bythia,* all of which were, or are presumed to have been, attached to pumice or other solid object, lack both a stalk and test hairs. Even within this group some specimens of *Cnemidocarpa bythia* possess test hairs.

Most of the species in the collection are also remarkable for their rather small size; the only exception is in *Culeolus,* a genus which, significantly, has a very long stalk. We do not know the attitude of *Culeolus* in life, but the stalk is probably not rigid enough to hold the body off the bottom. It is however, sufficiently long and flexible to allow the body to move freely under the influence of water currents if these exist, or as the result of the periodic unstimulated contractions which have been observed in some ascidians. In either case the effect would be to prevent the body from sinking into the soft substratum, an event which would interfere with the filtering activity of the branchial sac. Those species which lie free on the surface of the ooze are able to stay on the surface by virtue of their coating of long test hairs. But as there may well be a limit to the

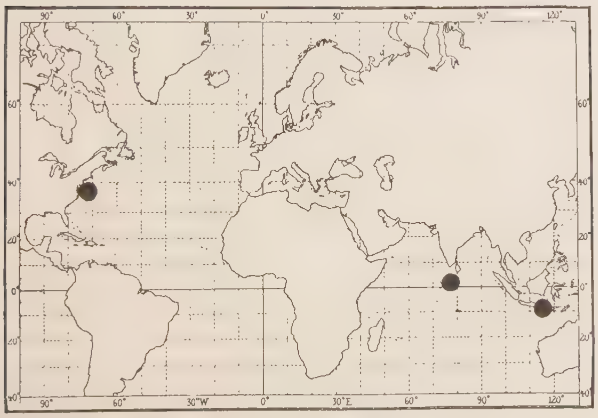


Fig. 15. Distribution of *Polycarpa albatrossi* (Van Name).

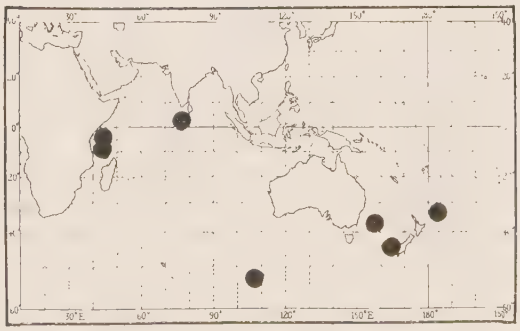


Fig. 16. Distribution of *Styela sericata* Herdman.

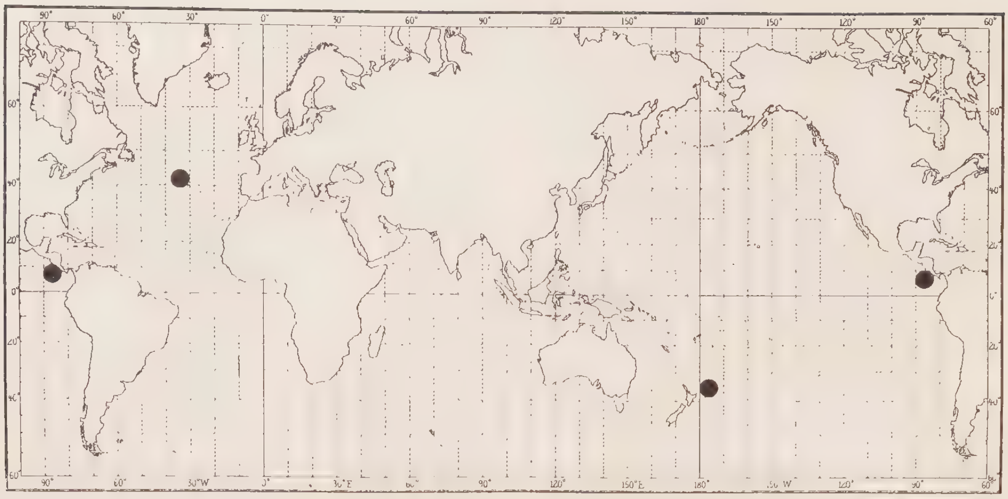


Fig. 17. Distribution of *Dicarpa simplex* Millar.

weight of body which this mechanism can support, these species are perhaps prevented from attaining a large size, and this, rather than a shortage of food, may be the limiting factor.

The larva of *Distaplia galatheae* shows, in the loss of the ocellus, the elimination of an organ which is no longer useful in the total darkness of deep water.

Another kind of adaptation concerns the method of feeding. The Ascidiacea evolved in comparatively shallow water and are adapted to life in waters rich in phytoplankton. The filter-feeding habit is related to these conditions and when certain ascidians started to penetrate greater depths the decreasing quantity of phytoplankton presented them with difficulties. Most deep water species, however, are still filter-feeders and must find enough suspended food in the water. The stomach contents of specimens of *Culeolus suhmi* taken from nearly 5000 metres have been examined for me by Dr. M.W. Parke of the Plymouth Laboratory, to whom I am indebted for the following list of material identified.

(1) many frustules of diatoms,

(2) skeletons of Silicoflagellata, quite common,

(3) Coccolithophoridaceae- cells still with coccoliths round them, loose coccoliths, and apparently cysts of Coccolithophoridaceae, fairly frequent,

(4) pieces of the skeletons of Radiolaria, quite frequent.

(5) brown walled cells, 3 to 10 µ, similar to non-motile stages of the genus *Chrysochromulina*, very frequent.

(6) various plant cells, apparently naked, possibly cells which have lost their coccoliths, other Chrysophyceae and occasional Dinoflagellates.

It appears from this list that *Culeolus* is a phytophagous filter-feeder and the same is probably true of many other deep water ascidians. The source of food material is presumably the slow rain of cells from the upper layers of water.

Most ascidians that have penetrated the depths have thus done so without fundamentally changing their method of feeding. The existence of quite different feeding methods in the two abyssal genera *Octacnemus* and *Hexacrobylus*, however, indicates that there exist considerable difficulties for filter-feeding animals at great depths, and that these difficulties have applied selective pressure favouring methods of feeding in which larger single organisms are taken. Although these two genera are the only

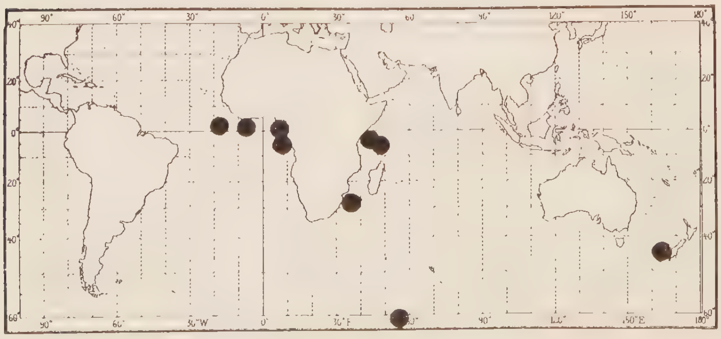
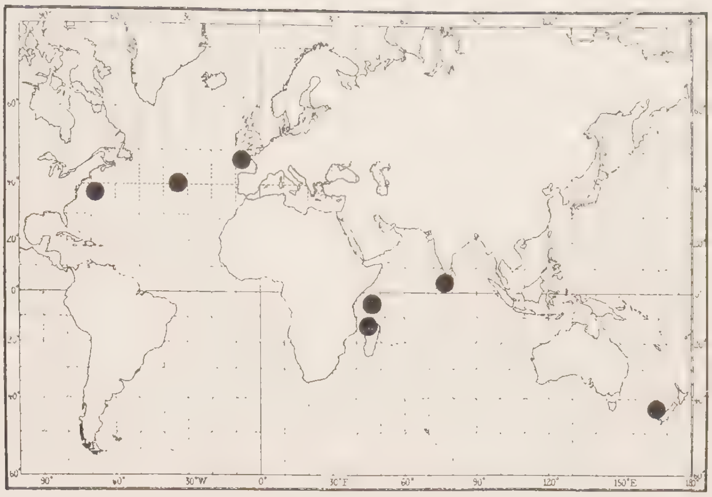


Fig. 18.
Distribution of *Bathystyeloides enderbyanus* (Michaelsen).

Fig. 19.
Distribution of *Culeolus suhmi* Herdman.



ones in which we have direct evidence, in the form of stomach contents, of a change from filter feeding, it is likely that some other abyssal genera showing similar anatomical modifications have similarly modified feeding habits. Thus in *Dicopia* and *Megalodicopia* the oral siphon is much enlarged and the pharynx has no true ciliated stigmata. These abyssal ascidians have probably the same feeding method as *Octacnemus* and *Hexacrobylus*. There is in addition one ascidian known from relatively shallow water, *Oligotrema psammites* Bourne, which feeds on quite large individual amphipod and copepod crustaceans and which shares with *Octacnemus* and *Hexacrobylus* the reduction of the pharynx and the enlargement of the oral siphon. It is possible that *Oligotrema* evolved in deep water where it acquired these adaptations and that it subsequently spread to shallower water.

Only one of the species in the collection is compound, and it appears that conditions in deep water favour solitary rather than compound forms.

Three possible reasons for this are suggested. The first is the relative scarcity of large solid objects over which compound ascidians can spread, an extended horizontal sheet being a common habit, especially in the *Didemnidae, Polyclinidae* and *Botryllinae*. The second possible reason concerns the interference with efficient filtering which the small zooids of compound forms might suffer living in the soft interface between ooze and overlying water. The solitary forms, having more powerful musculature, may be better able to deal with an excess of suspended matter in their feeding current.

The third factor which may act against compound forms is connected with their reproductive capacity. It is characteristic that the colonial habit involves reduction in size of the individual. It is also commonly associated with a diminished number of eggs in each zooid, although the eggs are given an increased chance of surviving to found a new generation by their retention within the zooid or colony until they have developed into advanced larvae. Retention within the parent is of positive survival value in shallow water where many pelagic larvae are lost through predation by plankton-feeding animals, or through their being carried by water currents away from localised favourable conditions. In deep water, however, loss by predation is small, and as the sea-floor is uniform over large areas, larvae are unlikely to be carried by currents to an unfavourable place by the time they are ready to settle. Solitary forms retain their capacity to produce large numbers of eggs and the fact that there is a longer pelagic period before settlement is not a disadvantage in deep water. Therefore from this point of view also, compound species are at a disadvantage compared with solitary species. It may be that all three factors play a part in determining the relative scarcity of compound species.

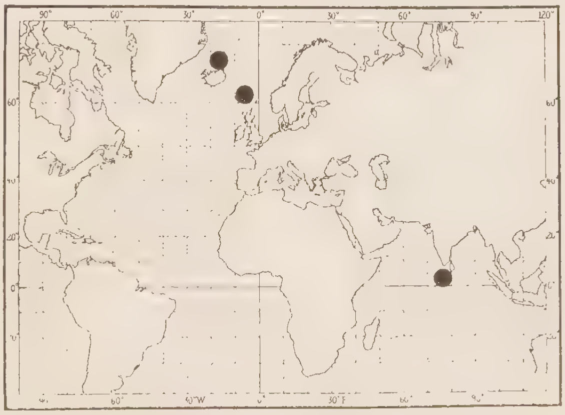


Fig. 20. Distribution of *Hexacrobylus indicus* Oka.

E.

List of species of ascidians recorded from depths of more than 2000 metres

	South Polar Sea	North Polar Sea	Atlantic Ocean	Indian Ocean	Pacific Ocean	Depth in metres
Family Clavelinidae						
Distaplia galatheae sp. n.	—	—	—	—	+	4410
Family Polyclinidae						
Pharangodictyon mirabile Herdman	—	—	—	+	—	2880
Family Didemnidae						
Leptoclinides faröensis Bjerkan	—	+	+	—	—	0-2847
Family Octacnemidae						
Octacnemus bythius Herdman	—	—	—	—	+	1957-2640
O. herdmani Ritter	—	—	—	—	+	4063-4087
Family Corellidae						
? Chelyosoma inaequale Redikorzev	—	—	—	—	+	985-3638
Abyssascidia wyvillii Herdman	—	—	—	+	+	4680-5900
Corynascidia suhmi Herdman	+	—	—	+	+	2475-4636
Benthascidia michaelseni Ritter	—	—	—	—	+	3927
Family Agnesiidae						
Agnesia depressa Millar	—	—	+	—	—	5850-5860
Family Ascidiidae						
Bathyascidia vasculosa (Herdman)	—	—	—	+	—	3510
Family Hypobythiidae						
Hypobythius calycodes Moseley	—	—	—	—	+	5220
Family Styelidae						
Hemistyela pilosa Millar	—	—	+	—	—	5250-5300
Cnemidocarpa drygalskii (Hartmeyer)	—	—	—	—	+	3310
C. bathyphila Millar	—	—	+	—	—	5250-5300
C. bythia (Herdman)	—	—	—	+	+	4510-7000
Polycarpa albatrossi (Van Name)	—	—	—	+	+	2599-4350
Styela sericata Herdman	—	—	+	+	+	3510-5860
S. milleri Ritter	—	—	—	—	+	425-4080
S. pusilla Herdman	—	—	—	—	+	3090
S. squamosa Herdman	—	—	—	+	—	4680
S. bathybia (Bonnevie)	—	+	—	—	—	2195
Dicarpa simplex Millar	—	—	+	—	+	2470-4600
Bathyoncus discoideus Herdman	—	—	—	—	+	4140
B. herdmani Michaelsen	+	—	—	—	—	4636
B. minutus Herdman	—	—	—	—	+	5625
B. mirabilis Herdman	—	—	—	+	—	2880
Bathystyeloides enderbyanus (Michaelsen)	+	—	+	—	—	2550-5300
Family Pyuridae						
Bathypera splendens Michaelsen	+	—	—	—	—	350-4636
Fungulus antarcticus Herdman	+	—	—	—	—	4473
F. cinereus Herdman	—	—	—	+	—	2880
Culeolus moseleyi Herdman	—	—	—	—	+	4365
C. murrayi Herdman	+	—	—	—	+	3397-4636
C. pyramidalis Ritter	—	—	—	—	+	4010-4066
C. recumbens Herdman	—	—	—	+	—	2475-3594
C. suhmi Herdman	—	—	+	+	+	2894-4820
C. willemoesi Herdman	—	—	—	—	+	4140
C. inversus Oka	—	—	—	—	+	3500
C. perlatus Herdman	—	—	—	+	—	2880
? Heterostigma singulare (Van Name)	—	—	+	—	—	5005

	South Polar Sea	North Polar Sea	Atlantic Ocean	Indian Ocean	Pacific Ocean	Depth in metres
Family Hexacrobylidae						
Hexacrobylus indicus Oka	—	+	+	+	—	891-4350
Family Molgulidae						
Molgula bathybia (Hartmeyer)	+	—	—	—	—	4636
M. immunda (Hartmeyer)	—	—	—	—	+	1788-4410
M. verrilli (Van Name)	—	—	+	—	—	3184
M. galatheae sp. n.	—	—	+	—	—	2550-5160

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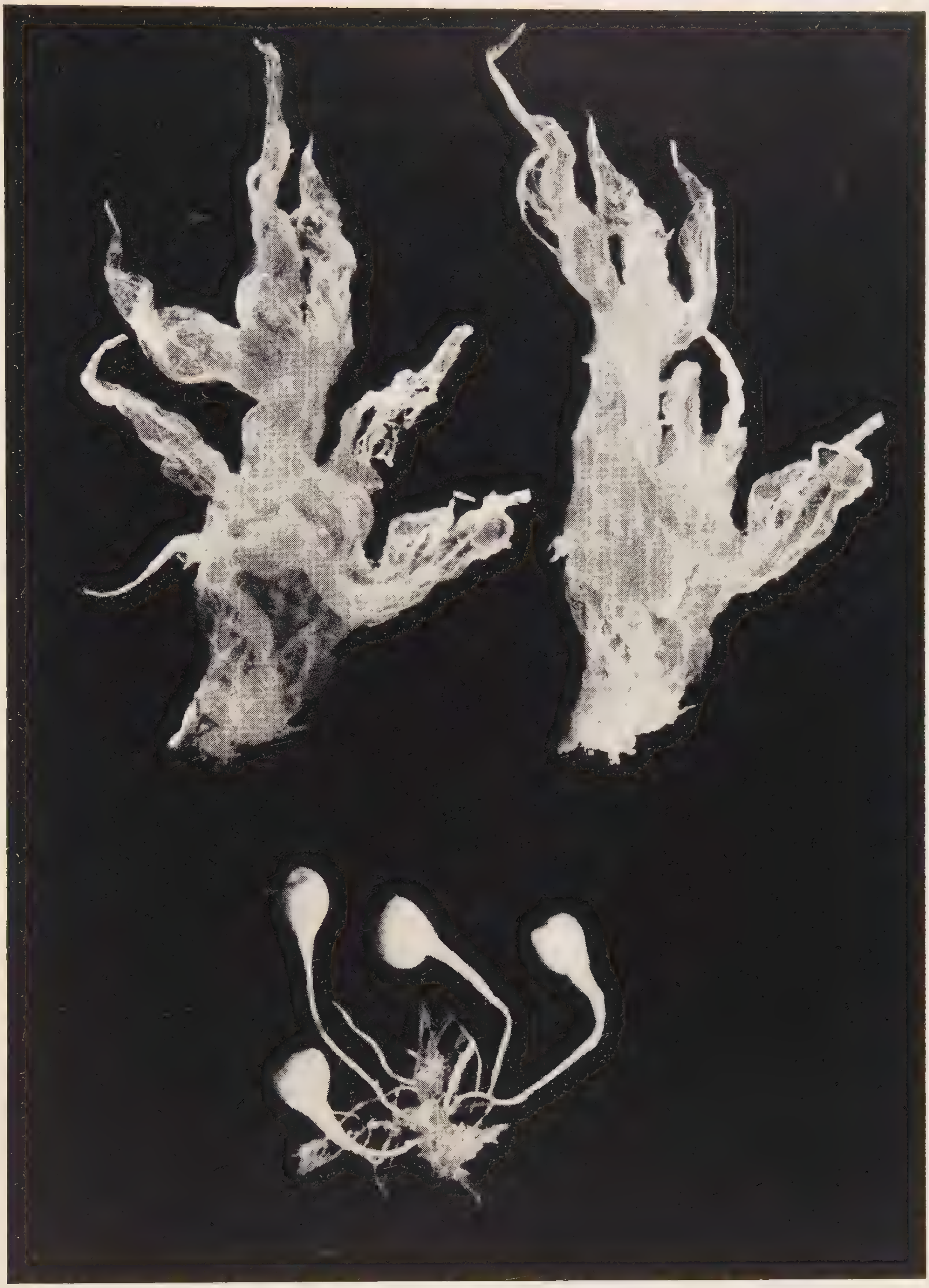

Plate 1, fig. 1, *Octacnemus bythius* Moseley. Photograph of intact animal, from the dorsal side; fig. 2, photograph of intact animal, from the left side; fig. 3, *Dicarpa simplex* Millar, a group of intact animals.

AMPHIPODA

FROM DEPTHS EXCEEDING 6000 METERS

By ERIK DAHL
Zoological Institute, Lund, Sweden.

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INTRODUCTION

The harvest of amphipods from the deep sea trenches brought back by the "Galathea" was comparatively rich, and i. a. establishes a new depth record for amphipods. A high percentage of the deep sea forms were previously unknown.

Thus the collection of fifteen species covered by the present report contains three genera and ten species new to science. Despite the comparatively great number of new forms, however, nothing essentially new is added to our knowledge of amphipod morphology and taxonomy, on the whole the hadal amphipods conform well with the structural patterns of the types found in ordinary abyssal depths. Some notes on the general morphology of the species dealt with will be found on p. 240.

One of the most difficult problems is to decide whether a species is pelagic or not. On the whole only such species which may be at least facultatively benthic are considered in the present survey, an exception being *Halice secunda* (STEBBING) (= *H. aculeata* CHEVR.) which is probably purely pelagic but was included because it came from a sample where benthic species were also present.

The writer is indebted to Dr. ANTON BRUUN and Mr. TORBEN WOLFF of the Zoological Museum, Copenhagen, for the permission to work on this unique collection and for the numerous ways in which they helped to make his work easier. My cordial thanks are also due to Dr. HANS KAURI, Lund, who helped me with translations of Russian literature and to my wife who made my drawings ready for publication.

SYSTEMATIC PART

FAMILY LYSIANASSIDAE

Genus **Hirondellea** Chevreux

syn. **Tetronychia** Stephensen.

Undoubtedly BARNARD (1930 p. 319) was right in making the genus *Tetronychia* Stephensen a synonym of *Hirondellea* Chevreux. This genus thus comprises six species, viz. *H. trioculata* Chevreux, *H. brevicaudata* Chevreux, *H. abyssalis* (Stephensen), *H. antarctica* (Schellenberg), *H. gigas* (Birstein and Vinogradov), and *H. dubia* n. sp., which is to be described below. *H. gigas* is also represented in the present collection.

Hirondellea dubia n. sp.

St. 656, Kermadec Trench, 35°20′S 178°55′W, type of bottom not noted, 7640-7680 m. 20. II. 1952. 1 specimen, 13 mm, probably ♂.

It is only with considerable hesitation that I refer the present specimen to a new species. Undoubtedly it is closely related to *H. brevicaudata* Chevreux, and the mutual relationship between the two becomes still more complicated through the present specimen being a male while the numerous specimens examined by CHEVREUX were probably all females. This might account for the differences in the structure of the antennula. On the other hand the absence of pigment and very poor development of the eyes, the different proportions of the segments of the first pereiopod, and the notably different palm of the same appendage as well as the broader and more deeply excavate fourth coxal plate of the present specimen combined to convince me that the specimen should at least provisionally be described as a new species. At least it seemed preferable to do so than to create a highly dubious synonym. As already pointed out, however, the different structure of the antennula and also that of the first gnathopod may be secondary sexual characters and consequently less significant than they appear to be. The specific name *H. dubia* refers to my doubts about its validity.

Description:

Body not carinate. No distinct eyes but the peculiar whitish band with yellowish dots which runs from the lateral lobes across the dorsal side of the head may represent rudimentary eyes. Lateral lobes prominent, very broadly rounded. Epistome broadly rounded, projecting in front of labrum.

First mesosome segment only slightly longer than subsequent segments.

First urosome segment with deep dorsal excavation, posterior margin slightly produced so that in the straight position assumed by the present specimen it completely covers the dorsal side of the second urosome segment which is extremely short. Posterior corner of third epimeral plate slightly produced but rounded.

Telson only little longer than broad, cleft to about one quarter of its length, lobes broad and terminally notched with two minute, subterminal setae in the notches.

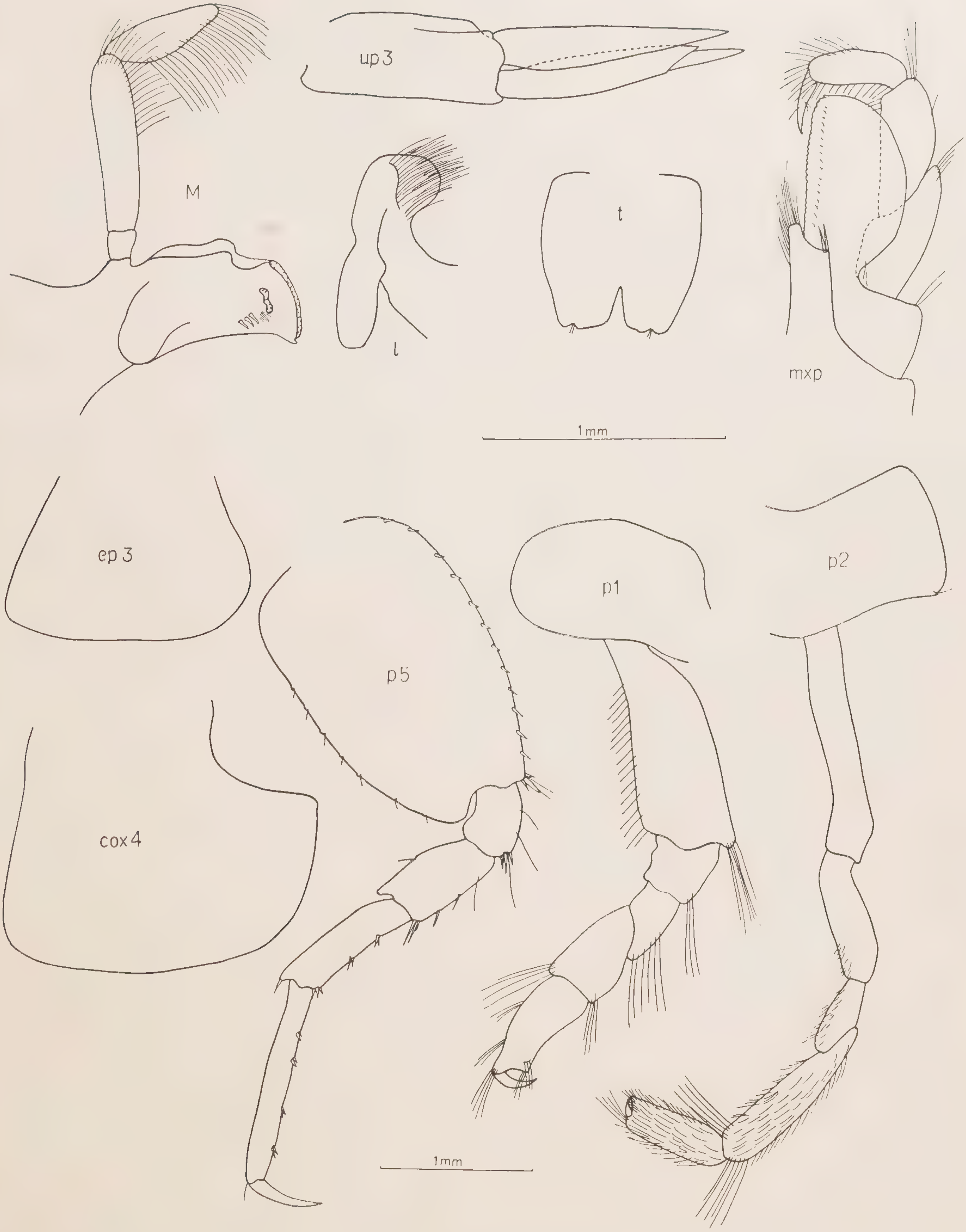
First segment of antennular peduncle carinate along the dorsomedial margin and about three times as long as the combined length of the two distal peduncular segments. Flagellum with 16 segments, the first of these segments elongate. Accessory flagellum of 6 segments the first of which is dorsoventrally flattened and as long as the first flagellar segment.

Antenna with last segment of peduncle only slightly shorter than fourth segment, flagellum consisting of about 20 segments.

Mouth parts closely resembling those of *H. abyssalis* as drawn by STEPHENSEN (1923 fig. 8 p. 64) but mandibular palp inserted above anterior part of molar (not in front of molar as in *H. abyssalis),* palp of maxillula with numerous terminal spines.

First coxal plate oval with posterior half (but not anterior corner) covered by second coxal plate. Basis of first gnathopod distinctly shorter than remainder of appendage, ischia and merus not notably short. Carpus broader than metacarpus and tapering distally, palm oblique and slightly sinuate, well defined and much shorter than dactylus. Second coxal plate slightly expanded distally, carpus of second gnathopod about twice the length of metacarpus. Distal corner of metacarpus somewhat produced so that the hand becomes intermediate between the subchelate and chelate types.

Fourth coxal plate about as broad as deep, deeply excavate behind. Fifth coxal plate with anterior and posterior lobes equally deep. Five posterior pairs of pereiopoda rather slender, P 6 longer than P 5 and P 7. Basis of last three pairs expanded but not very broad.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p1
p2
cox4
1mm

Fig. 1. *Hirondellea dubia* n. sp.

Uropods with slender rami, inner ramus of second uropod without constriction, third uropod with rami nearly equal.

Hirondellea gigas (Birstein and Vinogradov 1955)
syn. **Tetronychia gigas** Birstein and Vinogradov 1955

St. 418. Philippine Trench. 10°13′N 126°43′E, clay with gravel and stones, 10.190-10.150 m. 21. VII. 1951. 1 specimen, about 22 mm.
St. 429. Philippine Trench. 9°49′N 126°44′E. 10.020-10.120 m. 2. VIII. 1951. 3 specimens 20-25 mm.

The two records of this species establish the depth record as far as amphipods are concerned. Obviously, however, the species is at least facultatively bathypelagic, for Birstein and Vinogradov (1955 p. 228) record specimens captured by means of plankton nets. The excellent drawings published by the two Russian writers leave no doubt about the specific identity of the specimens from the Philippine and the Kurile-Kamtchatka trenches. As their description is entirely in Russian it appears convenient to give here a re-description of the species based upon the "Galathea" specimens. Drawings of some relevant appendages are also included.

Body smooth, not carinate apart from a rounded ridge behind a transversal depression on the first urosome segment. Cephalon with lateral corners produced and very broadly rounded. Epistome projecting past the labrum as a very broadly rounded ridge. Large and somewhat irregular markings on the sides of the head may indicate the presence of eyes, but their outline could not be traced in the preserved specimens.

First epimeral plate with posterior margin evenly rounded, second plate with posterior corner rectangular, third plate with hind margin straight but somewhat oblique so that the corner is somewhat produced with the point rounded.

Telson distinctly longer than broad with a few hairs on dorsal surface, cleft to about one third of its length. Apical lobes entire and without any marginal spines.

Antennula not much shorter than antenna, first segment of peduncle longer than second and third segments combined. Flagellum consisting of about 22 somewhat indistinct segments, first segment as long as the three to four subsequent ones combined. Accessory flagellum with 7 segments, the first of which is as long as the three subsequent ones together.

Antenna with basal segment of peduncle dilated, externally visible, about as long as broad, and about three times as broad as the second and third segments. Two distal segments of peduncle subequal.

Outer plate of maxillula with 11 serrate and pectinate spines, some of the former very broad, palp with 10 blunt teeth and some slender spines. Maxilla with both plates of about equal width. Maxilliped with outer plate very broad, inner plate with distal margin sinuate with two slender spines on lateral corner.

First coxal plate with anterior distal corner visible in front of second coxal plate and obtusely rectangular. Fourth coxal plate deeply excavated behind to receive fifth coxal plate.

First gnathopod with anterior margin of basis setose. Metacarpus as long as carpus and with posterior margin slightly concave. Palm transverse, straight and setose and provided with four chelate spines at posterior corner. Dactylus longer than palm with five teeth and a few setae on posterior margin.

Second gnathopod with carpus and metacarpus densely setose. Metacarpus with posterior corner produced but blunt, provided with a few large spines and numerous smaller ones which are at least partly brush-like. Dactylus with one tooth on posterior margin and longitudinal rows of small spines both on medial and lateral side.

Third and fourth pereiopods comparatively stout. Fifth to seventh pereiopods with basal segment expanded but otherwise slender. Accessory branchiae are present at least on the branchiae of P5 and P6, possibly also on P7.

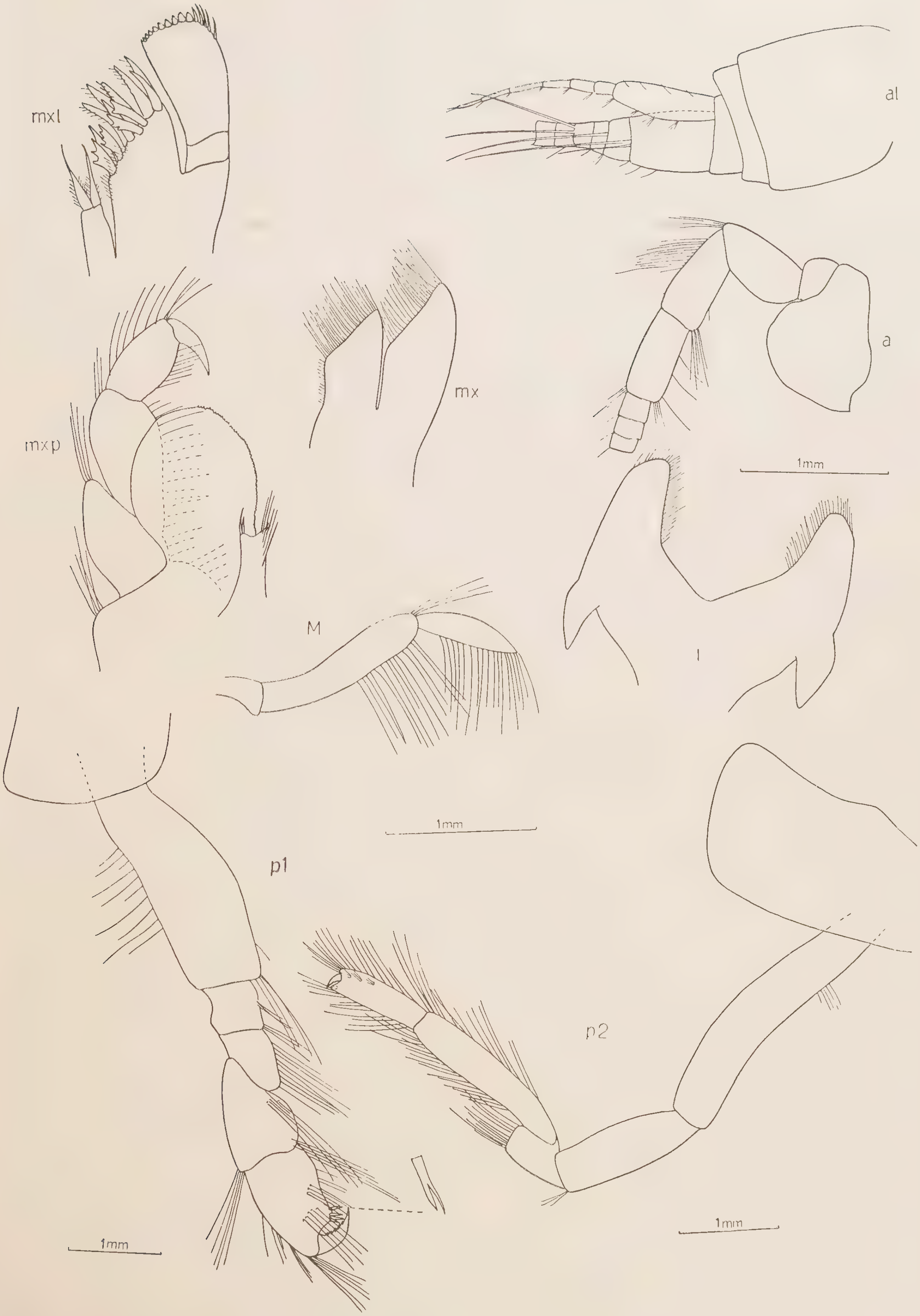
First uropod long and slender. Second uropod without any constriction in the neighbourhood of the apex of inner ramus. There is a row of spines along the dorsal margin of the basal segment and both rami. Third uropod with a dorsolateral flange and a transverse row of numerous spines near distal end of dorsal margin of basal segment. A double row of spines along dorsal margin of inner ramus and a shorter row of spines along distal part of ventral margin. Second segment of outer ramus much narrower than first segment.

Genus **Onesimoides** Stebbing.

Onesimoides cavimanus Pirlot 1933.

St. 497. Banda Trench 5°18′S 131°18′E, soft clay, 6490-6650 m. 23. IX. 1951. 1 ♂ about 12 mm.

This is the second specimen of the species. The type was collected by the "Siboga" Expedition also in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al
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M
l
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p1
p2
1mm
1mm

Fig. 2. *Hirondellea gigas* (Birstein & Vinogradov).

the Banda Sea in a depth of 1158 m (PIRLOT 1933 p. 129).

In general appearance and most structural details the present specimen agrees perfectly with the descriptions given by PIRLOT, and especially the most characteristic shape of the first gnathopod leaves no doubt about their specific identity. The present specimen is broken at the border between the second and third mesosome segments, but there can be no doubt about the two parts belonging to the same specimen, for they fit each other perfectly.

Some minor discrepancies between the present specimen and the drawings and descriptions given by PIRLOT may deserve mentioning. Both the "Galathea" and the "Siboga" specimens are males, the "Galathea" specimen is a good deal larger than the other.

In the present specimen the posterior margin of the first epimeral plate is not excavate, instead it bulges a little backwards, but on the other hand the anterior margin is distinctly excavate. In the second plate the anterior margin is almost straight but the posterior margin bulges a little, like that of the first plate. The posterior margin of the third plate is straight and the posterior corner is subacute without being produced.

In the type specimen the first and second epimeral plates are represented as bulging forwards and excavate behind, while in the third plate the anterior margin is represented as being straight and the posterior as being rounded below a slightly sinuate posterior margin.

The difference in this respect between the two specimens might appear important enough if it were not for the fact that if for each separate plate in PIRLOT's drawing the orientation is changed so that the present anterior margin becomes posterior and vice versa the two sets become identical.

I think we are forced to accept the view that PIRLOT became confused over the orientation of the dissected parts on his slides and that the actual shape of the epimeral plates of the two specimens is similar.

The flagellum of the antennula of the present specimen has got 12 segments as compared with 14 in the type, and the corresponding figures for the antennar flagellum are 11 and 13 respectively.

The hand of the first gnathopod seems to be longer and narrower in the present specimen than in the type and the dense growth of hairs seems to be more marginal.

As already pointed out, however, the minor descrepancies mentioned here could hardly be said to make the specific identity of the two specimens in any way doubtful.

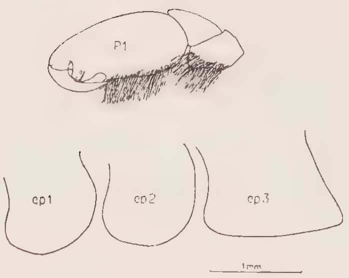

Fig. 3. *Onesimoides cavimanus* Pirlot.

Genus **Schisturella** and the **Ambasia** group

Among the amphipods from the Kermadec Trench was one ovigerous female about 10 mm in length, which, thanks to the redescription of *Schisturella pulchra* given by SHOEMAKER (1930), could be identified as a new species of the genus *Schisturella*.

The genus *Schisturella* shows a considerable degree of similarity with several of the genera which together could be said to constitute the *Ambasia* group. Of these *Parambasia* Walker and Scott and *Pseudambasia* Stephensen are closely related but stand a little apart from the others on account of their large first coxal plate which is much wider distally than proximally and not covered by the second coxal plate (cf. STEPHENSEN 1927 fig. 5 p. 305).

There remain the following genera, viz. *Ambasia* Boeck 1870, *Schisturella* Norman 1900, *Metambasia* Stephensen 1923, *Ambasiopsis* Barnard 1931, and *Ambasiella* Schellenberg 1935. Most of these genera are monotypic, and only one, *Ambasiopsis,* consists of as many as three species. It seems, however, as if *Ambasiopsis,* too, will have to be divided into two genera, and as this division has a certain bearing upon *Schisturella* it is necessary here to deal with it in some detail.

BARNARD's final definition of *Ambasiopsis* (1932, p. 44) runs as follows: "Agreeing with *Metambasia,* Steph. 1923, but differing as follows: 1st gnathopod feebly subchelate, outer plate of maxilliped non-spinose, inner ramus of uropod 2 not constricted, peraeopods 3-5, especially 5, much shorter and 4th joint more expanded, 3rd joint of antenna 2 not expanded. The last character is privisional as the only ♂ (see *uncinata, infra)* may not have attained its adult characters."

Although no drawings were given of the mouth parts the description of *A. georgiensis* comprises all relevant details and is very lucid. *A. uncinata* is said to resemble *A. georgiensis* closely.

Nicholls (1938 p. 20) points out that the inclusion of his new species *A. tumicornis* "requires a slight modification of Barnard's diagnosis, inasmuch as in it the outer plate of the maxilliped is spinose, as in *Metambasia,* and the first gnathopod is definitely subchelate," The description of the new species, however, contains various important points in which *A. tumicornis* differs from *A. georgiensis.* Thus in the palp of the mandible the two distal segments are subequal, and the maxillular palp also is rather different. The inner lobe of the maxillula has only one seta (in *A. georgiensis* there are two long and one short setae) and the telson is "scarecely longer than wide, cleft for two-thirds of its length."

To me it seems impossible to retain *A. tumicornis* within the genus *Ambasiopsis* without violating the current concept of generic delimitation within the group. The question then arises whether the species could be referred to any of the other genera. Apparently the shape of the maxilliped closely recalls that of *Metambasia* and *Schisturella,* and this is the case also with the epistome and labrum. On the other hand the first gnathopod is definitely subchelate while that of *Metambasia* is simple. In *Schisturella* the first gnathopod is subchelate but the shape of the mandibular palp, the armature of the inner plate of the maxillula, the shape of the fifth to seventh pereiopods (which are said to resemble those of *A. georgiensis)* preclude the inclusion of *A. tumicornis* into either *Schisturella* or *Metambasia. A. tumicornis* also lacks the terminal spine of the first segment of the antennular flagellum which is found in both species of *Schisturella.* It seems inevitable to create a new genus to receive *Ambasiopsis tumicornis* Nicholls, and for this genus I propose the name *Neoambasia,* to be defined below.

The result is that the *Ambasia* group in the stricter sense will consist of six genera, four of which are monotypic while the other two have two species each. Although such a state is not very agreeable and throws certain doubts upon the taxonomic principles now adopted it is hardly possible to make a revision of these principles for this generic group alone. A revision, which appears justified and even desirable, will have to comprise the whole family Lysianassidae, but such an enterprise would demand a very large effort and lies outside the scope of the present paper.

It seems necessary to review once more the generic definitions within the *Ambasia* group and to make the adjustments which are indicated by the facts accumulated during the latest decades.

Genus **Ambasia** Boeck

Definition as given by Stebbing (1906 p. 51).

Species: *A. atlantica* (Milne-Edwards).

Stebbing's definition only applies to *A. atlantica,* for he was not aware of the different shape and armature of the epistome and maxilliped of *A. pulchra* Hansen (now *Schisturella pulchra),* nor did he mention that the first gnathopod of the latter species is feebly subchelate. *A. murmanica* Brüggen was only added in the appendix to Stebbing's monograph, and the important characters in which it differs from *A. atlantica* were not commented upon. For this reason no alterations of Stebbing's diagnosis are necessary.

Genus **Schisturella** Norman

Shoemaker (1930 p. 13 ff.) gave a redescription of *S. pulchra* (Hansen) and produced a complete set of excellent drawings. He also corrected some mistakes made by Norman (1900 p. 208) which enables us to define the genus in the following manner.

Definition: Resembling *Ambasia.* First coxal plate very small, roughly triangular and almost completely hidden below second coxal plate, epistome straight or not very prominent, labrum somewhat produced forwards-upwards. First segment of antennular flagellum with long terminal spine. Mandible with palp attached over molar, second segment distinctly longer than third, molar strong. Maxillula, inner plate with two terminal setae, outer plate with numerous (11) serrate or pectinate spines, palp well developed. Maxilla, inner plate somewhat shorter than outer. Maxilliped with dactylus of palp well developed, outer plate not reaching end of second segment of palp, with spines on distal margin. First pereiopod with palm oblique. Fifth to seventh pereiopods with distal parts rather slender. Telson distinctly longer than broad, deeply cleft.

Species: *S. pulchra* (Hansen)
S. galatheae n. sp. (to be described below).

Genus **Metambasia** Stephensen

Definition: Very near *Schisturella.* Agreeing with definition given above except in the following respects, viz. no terminal spine on first segment of

Table 1.

	Ambasia	*Schisturella*	*Metambasia*	*Ambasiopsis*	*Ambasiella*	*Neoambasia*
Cox 1	Rather short not triangular	Rather or very short, triangular	Very short, triangular	Not very short triangular	Not very short triangular	Not very short oval
Epistome	Projecting, flanged	Straight or slightly projecting	Straight	Straight	Straight	Straight
Labrum, dorsoanterior lobe	Present	Present	Present	Present	Absent	Present
Mandible, palp attached	Behind molar	Over molar	Over molar	Over molar	Behind molar	?
Mandible, palp $\frac{\text{segm. 3}}{\text{segm. 2}}$	Abt. $^2/_3$	Abt. $^2/_3$	Abt. $^2/_3$	Abt. $^2/_3$	Abt. $^1/_3$	Abt. $^1/_1$
Mandible, molar	Weak	Strong	Strong	Strong	Weak	?
Maxillula, setae on inner plate	2	2	2	3	2	1
Maxilliped, palp	Rather narrow	Rather narrow	Rather narrow	Broad	Very broad	?
Maxilliped, spines on outer plate	Absent	Present	Present	Absent	(Setae)	Present
First gnathopod	Simple	Subchelate	Simple	Weakly subchelate	Simple	Subchelate
Telson	Length $>$width, cleft $^2/_3$	Length $>$width, cleft $^3/_4$ or more	Length $>$width, cleft $<^2/_3$	Length $>$width, cleft $^3/_4$	Length $>$width, cleft $^3/_4$	Length $=$ width, cleft $^2/_3$

antennular flagellum, first pereiopod simple, telson less deeply cleft.

Species: *M. faeroensis* Stephensen.

The relationship between *Schisturella* and *Metambasia* appears in fact to be so close that it is only with some hesitation I maintain *Metambasia* as a separate genus. The most important difference is to be found in the first gnathopod which is simple in *Metambasia* but subchelate in *Schisturella* and on the whole of a rather different shape.

Genus **Ambasiopsis** Barnard

Barnard's definition (1931 p. 425, 1932 p. 44, already quoted above p. 216) is rather brief. His description of *A. georgiensis* however, is rather extensive, especially where the mouth parts are concerned. As *A. uncinata* is said closely to resemble *A. georgiensis* it seemed justified to compile the following diagnosis.

Definition: Resembling *Schisturella.* First coxal plate subtriangular, not very short, anterior corner covered by second coxal plate but larger part of anterior margin visible. Epistome not protruding, labrum produced. Mandible as in *Schisturella.* Maxillula with two long and one short terminal setae on inner plate, palp narrow with only few spinules. Outer plate of maxilliped minutely serrate but lacking spines. First gnathopod feebly subchelate, three posterior pairs of pereiopods rather short and stout, telson rather deeply cleft.

Species: *A. georgiensis* Barnard
A. uncinata Barnard.

Genus **Ambasiella** Schellenberg

Definition: First coxal plate subtriangular, almost completely hidden, not very short. Epistome and labrum straight, mandible very slender, palp attached behind molar, third segment very short, only about $^1/_3$ of second. Maxillula, inner plate with two terminal setae, outer plate with numerous spines, palp narrow with few terminal spinules. Maxilliped with inner and outer plates very narrow, outer plate reaching nearly to end of second segment of palp and provided with numerous setae on medial margin, palp very broad, terminal segment very small. First pereiopod simple. Telson deeply cleft.

Species: *A. murmanica* (Brüggen).

Genus **Neoambasia** n. gen.

Definition: Resembling *Schisturella.* First coxal plate oval, almost concealed but not very short. Epistome straight, labrum projecting as in *Metam-*

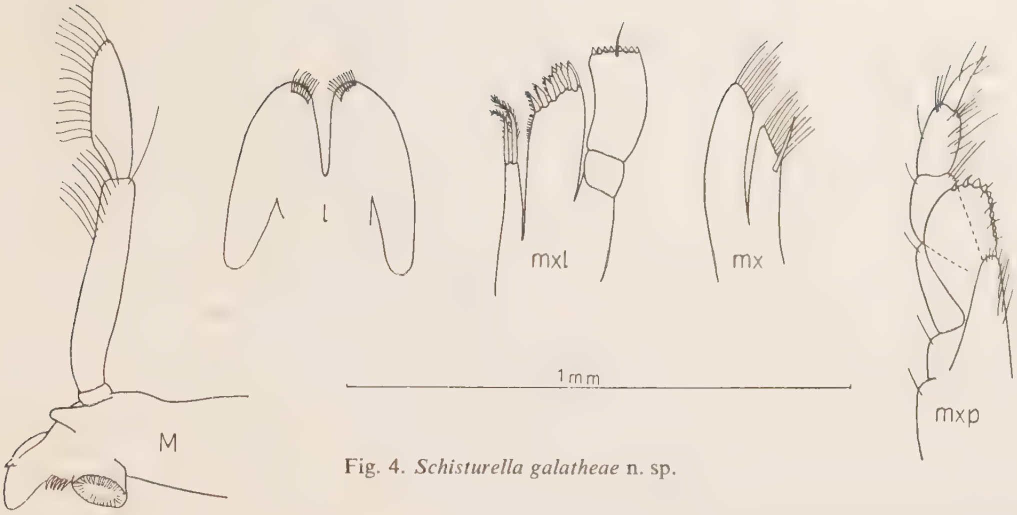

Fig. 4. *Schisturella galatheae* n. sp.

basia. Mandible resembling that of *Ambasiopsis* but with two distal segments of palp subequal. Inner plate of maxillula with one seta, palp with numerous (9) spines. Maxilliped, outer plate with numerous spines on medial margin. First pereiopod subchelate. Three last pairs of pereiopods resembling those of *Ambasiopsis*. Telson longer than broad, deeply cleft.

Species: *N. tumicornis* (Nicholls).

The above definition was compiled from the description of *Ambasiopsis tumicornis* given by NICHOLLS (1938 p. 21). That description is rather brief and consequently the generic definition may have to be supplemented in various respects.

To facilitate a comparison between the genera dealt with above, some of the most important features are compared in tabular form on p. 218.

Schisturella galatheae n. sp.

St. 651. Kermadec Trench, 32°10′S, 177°14′W, brown clay with pumice, 6960-7000 m. 16. II. 1952. 1 ♀ about 10 mm with 2 eggs.

No eyes. Lateral lobes of cephalon narrow with the points somewhat rounded. Epistome rounded, bulging a little so that it protrudes past the likewise rounded anterodorsal lobe of the labrum from which it is separated by a fold.

First urosome segment rather deeply excavated dorsally, third epimeral plate with posterior corner subacute, somewhat produced and with a rather indistinct tooth. Telson narrow, very deeply cleft, with three pairs of dorsal spines on the distal part of the lobes, the last pair subterminal.

Antennula with first segment dorsally carinate, second and third segments short. First and second segments of flagellum with a ventral, terminal, slender spine, in both cases as long as the two subsequent segments. Total number of segments seven. Accessory flagellum with five segments. Antenna slightly longer than antennula with fourth segment of peduncle longer than fifth segment. Flagellum with 12 segments.

Mandible with cutting edge rather long, with a small denticle near dorsal margin. Spine-row short, molar strong, palp attached over molar, first segment short, third segment about $^2/_3$ of second. Labium with inner margin of lobes straight. Maxillula, inner plate with two terminal setae, outer plate with 11 spines, the proximal ones of which are pectinate while the distal ones are serrate. Palp rather broad, reaching just past the spines of the inner plate and provided with 8 terminal spinules. Maxilla with plates rather narrow, outer plate distinctly longer.

Maxilliped with palp not very broad, dactylus well developed. Outer plates almost semicircular, reaching well past middle of second segment of palp. Armature very characteristic; on distal margin two curved spines and near anteromedial corner large denticles which continue along inner margin and decrease in size proximally. Inner plates with numerous setae on distal and inner margins.

First coxal plate triangular, rather short (but distinctly longer than in *S. pulchra)*. First gnathopod slender, distinctly subchelate with carpus slightly longer than metacarpus, posterior margin of metacarpus straight, palm oblique, well defined, with two spines at posterior corner. Second gnathopod slender, metacarpus a good deal shorter than carpus and hardly broader, distinctly subchelate with dactylus pectinate. All posterior pereiopods slender but basis of fifth to seventh pereiopod broad.

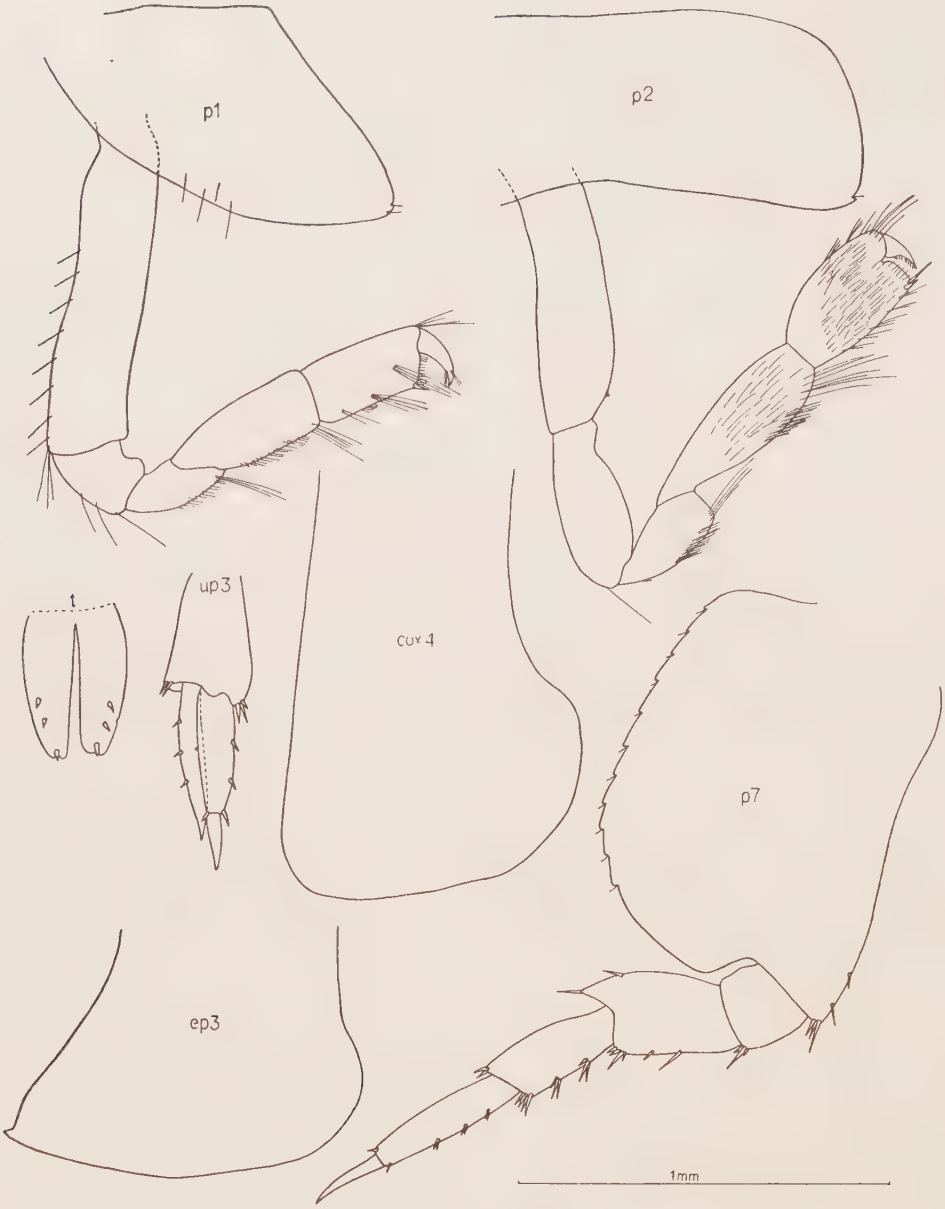

Fig. 5. *Schisturella galatheae* n. sp.

First uropod not reaching past second uropod, outer ramus of second uropod without constriction. Inner ramus of third uropod only a little shorter than outer ramus and distinctly longer than first segment of outer ramus.

S. galathea is easily distinguished from *S. pulchra* by means of various features, i. a. the longer first coxal plate, the palm of the first gnathopod which is much less oblique, the much larger denticles along the margin of the outer plate of the maxilliped, the absence of eyes and the presence of a long terminal spine also on the second segment of the antennular flagellum.

Bathycallisoma n. gen., the **Scopleocheirus** and **Alicella** groups

The genera *Scopelocherius* Bate, *Paracallisoma* Chevreux, *Aroui* Chevreux, and *Scopelocheiropsis* Schellenberg form a natural group of somewhat obscure mutual relationships. In all of them the first gnathopod is of a peculiar shape and strikingly similar. There is also a general agreement with respect to numerous other features, e. g. the mouth parts, the second gnathopod (which is more or less distinctly subchelate) etc. The fact that all genera except *Scopelocheirus* are monotypic makes the taxonomic evaluation of the various characters

Table 2.

	Scopelocheirus[1]	*Paracallisoma*[1]	*Aroui*	*Scopelocheiropsis*	*Bathycallisoma*
Epistome	Protruding	Not protruding	Not protruding	Protruding	Not protruding
Maxilliped, outer plate reaching	Middle of 2nd segm. of palp	Distal end of 2nd segm. of palp	Distal end of 2nd segm. of palp	3rd segm. of palp	Middle of 2nd segm. of palp
Maxilliped, 4th segm. of palp	Normal	Normal	Normal	Vestigial	Normal
P 1 and P 2, length	Equal	P 1<P 2	P 1<P 2	P 1<P 2	P 1<P 2
Coxal plates	Long	Rather short	Long	Short	Rather short
Basis of P 5-P 7	Broad	Rather narrow	Broad	Narrow	Broad
Merus of P 5	Normal	Normal	Broad	Normal	Normal

1. Schellenberg (1926 a p. 258) regarded *Scopelocheirus coecus* Holmes as a synonym of *Paracallisoma alberti* Chevreux, and the same veiw was adopted by Birstein and Vinogradov (1955 p. 223). The fine set of drawings of *S. coecus* produced by Barnard (1954 pl. 4 and 5) clearly shows that the species should be referred to *Paracallisoma*, but there are some discrepancies especially in the shape of the first coxal plate which may indicate that it is specifically different from *P. alberti*.

used to distinguish between them somewhat difficult. This difficulty is increased by a specimen captured by the "Galathea" which, although differing from all previously known forms, at the same time cuts across some of the border lines drawn between the different genera.

The specimen obtained by the "Galathea" very closely resembles the species of which fragments were obtained by the Swedish Deep Sea Expedition in the Puerto Rico Trench. Those specimens were in such a condition that Schellenberg (1955 p. 185) preferred not to give a definite description. He refers to the Puerto Rico specimens as "aff. Paracallisoma spec." There can be no doubt about the generic identity of the fragments identified by him and the species obtained by the "Galathea". There is indeed such a close resemblance with respect to the characters available for comparison that I am inclined to believe that they may even belong to the same species. The final decision on this point must wait, however, till more complete specimens of the Atlantic form become available.[1]

In table 2 a comparison is made between the four genera mentioned above and the "Galathea" specimen. As will be seen from table 2 the specimen obtained by the "Galathea" rather closely resembles the genus *Paracallisoma* from which it is distinguished mainly by the outer plate of the maxilliped which is comparatively shorter, and, above all, by the three posterior pereiopoda which are notably different.

Chevreux himself never gave any diagnosis of the genus *Paracallisoma*, but a brief diagnosis was given by Schellenberg (1926 p. 257). It seems to me that the difference in the proportions of the maxilliped is of comparatively minor importance and does not in itself justify the creation of a new genus to receive the "Galathea" specimen. On the other hand the difference in the shape of the three posterior pereiopoda is very striking and appears of to be doubly important because it underlines the re-

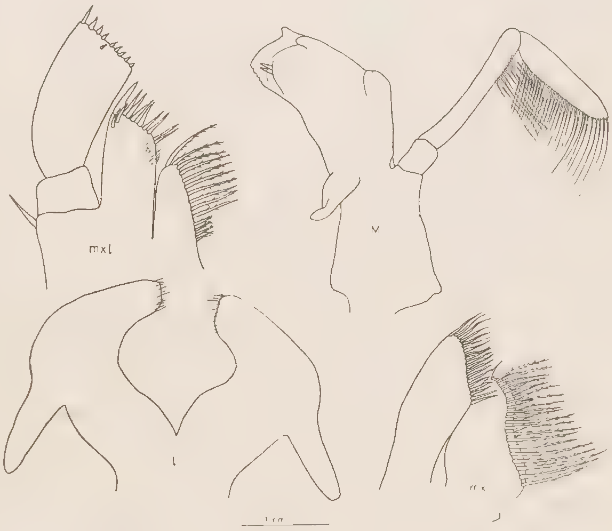

Fig. 6. *Bathycallisoma pacifica* n. gen. et sp.

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[1] After the present paper had already gone to press, Birstein and Vinogradov (1958) described a new species, *Scopelocheirus schellenbergi*, from the Pacific. Simultaneously I have had the opportunity to examine Schellenberg's specimen from the Atlantic. As far as I can see the latter are to be referred to *S. schellenbergi*. On the other hand the "Galathea" specimen differs, especially in the shape of the first gnathopod and some other minor characteristics, and must probably be kept apart as a separate species. According to the nomenclature used here *S. schellenbergi* should be called *Bathycallisoma schellenbergi*. If the present two species should be referred to *Scopelocheirus* several of the other genera referred to in table 2 should also be abolished. Therefore I think *Bathycallisoma* should be retained, at least provisionally.

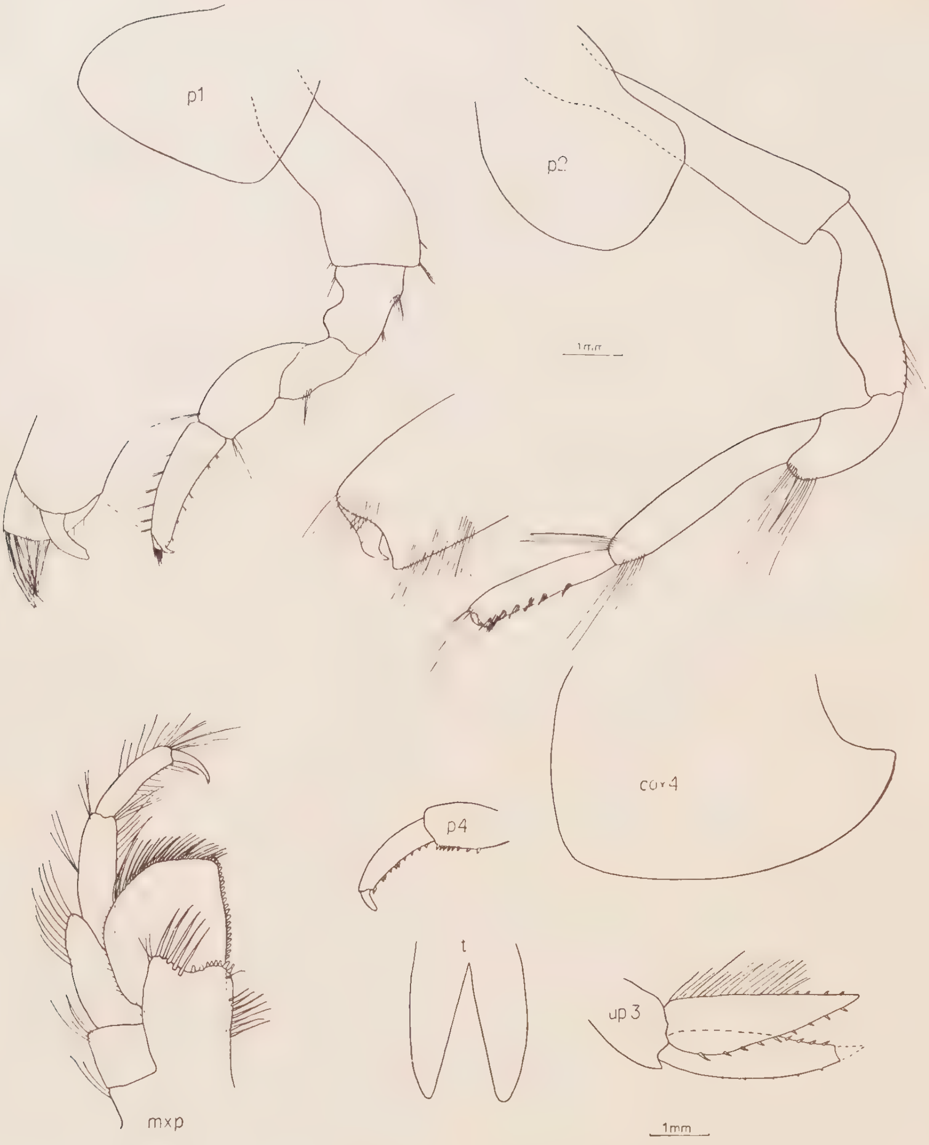


Fig. 7. *Bathycallisoma pacifica* n. gen. et sp.

lationship between the *Scopelocheirus* group (as defined above) and the *Alicella* group (consisting of the genera *Alicella* Chevreux and *Paralicella* Chevreux), a relationship which was pointed out by Chevreux (1935 p. 46).

The three posterior pairs of pereiopoda in the present specimen very closely resemble those of *Alicella* and *Paralicella* in having a broad basis and long and slender distal parts. In this way the present species becomes a very interesting connecting link between the two groups, and the creation of a new genus to receive it appears inevitable.

Bathycallisoma n. gen.

Resembling *Scopelocheirus* and *Paracallisoma* but coxal plates rather short, epistome straight and not protruding in front of labrum. Lower lip with medial margins of lobes sinuate. Maxilliped with outer plate reaching to middle of second segment of palp, fourth segment of palp well developed. Second gnathopod much longer than first gnathopod, three posterior periopoda with basis broad, distal parts long and slender. Telson cleft to base.

Bathycallisoma pacifica n. sp.

Syn. ? "aff. Paracallisoma spec". Schellenberg 1955.

St. 651. Kermadec Trench. 32°10′S 177°14′W, brown clay with pumice, 6960-7000 m. 16. II. 1952. 1 female about 33 mm, somewhat mutilated.

Body smooth, without dorsal carina. Cephalon shorter than first free mesosome segment. No rostrum. Lateral corners produced (though not as much as in *Paracallisoma alberti)* and obtusely pointed. No eyes visible in preserved specimen.

Posterior margin of third epimeral plate straight, posterior corner slightly produced. Telson cleft to base, unarmed.

Antennulae and antennae closely resembling those of *P. alberti.* Antennula short, reaching a little past middle of fifth segment of antennar peduncle. Peduncle heavy, basal segment with a high and narrow keel along dorsomedial margin. Flagellum with 10 segments, the first of which is long and provided with a dense ventromedial growth of setae. Accessory flagellum with three segments, first segment flattened, forming a thin and vaulted plate which is longer than the two distal segments together.

Antenna rather long, reaching approximately to posterior border of fourth mesosome segment. Flagellum with numerous segments.

Mandible with cutting edge long and narrow, spine-row probably represented by two short spines near the base of the cutting edge, molar a thin, jutting plate. Palp with second segment slightly longer than third segment.

Lower lip with inner margins of lobes deeply excavated.

Inner plate of maxillula with a row of plumose setae on inner margin, outer plate with a dense brush of short hairs near distal end of inner margin and 11 distal spines. Two of these spines are bent at the tip and provided with a few lateral denticles. Palp with two segments. last segment somewhat expanded distally.

Maxilla with plates of equal length, inner plate triangular.

Maxillipeds with palp long, outer plate reaching past the end of second segment of palp, inner plate with distal margin somewhat sinuate and with numerous hairs and denticles.

Coxal plates rather short. Second plate covering only posterior margin of first plate. Fourth plate excavated behind to receive fifth plate.

First gnathopod only half as long as second but much stouter. Basis of first gnathopod somewhat expanded distally, ischia about as broad as long and much wider than distal segments. Dactylus small with basal half concleaed between the projecting flanges of metacarpus. Second gnathopod slender, dactylus attached near centre of distal margin of metacarpus.

Third and fourth pereiopoda short and comparatively stout. Fifth and sixth pereiopods with basis about as long as broad and rounded posteriorly, distal segments long and slender. Seventh pereiopod with basis distinctly longer than broad, otherwise resembling two preceding pereiopods.

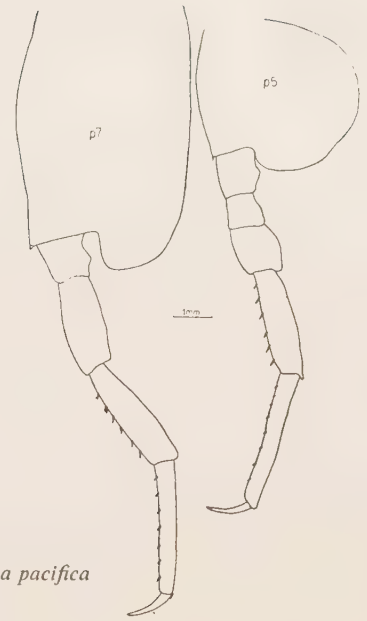


Fig. 8. *Bathycallisoma pacifica* n. gen. et sp.

All uropods with rami more or less lanceolate, third uropod with both rami somewhat damaged distally.

Genus **Tryphosa** Boeck

Tryphosa bruuni n. sp.

St. 658. Kermadec Trench. 35°51′S 178°31′W, brown sand with clay and stones, 6660-6770 m. 20. II. 1952. 1 female about 7 mm. 1 juv.

Cephalon with lateral lobe moderately produced, blunt. No eyes. Epistome nearly straight, upper lip projecting a little in front of it. Third epimeral plate with posterior margin straight, posterior corner produced but not forming any tooth. First urosome segment dorsally with a saddle-shaped notch and a very low carina posterior to it. Telson cleft to about two thirds of its length, with three pairs of dorsal spines, apices narrowly rounded without terminal spines.

Antennula and antenna subequal. Antennula with second segment of peduncle not very short, flagellum with nine segments. Accessory flagellum with three segments the first of which is long and dorsoventrally flattened. Antenna with fourth segment of peduncle distinctly longer than fifth segment.

Mandible with cutting edge smooth, spine-row with three spines only, molar large and protruding.

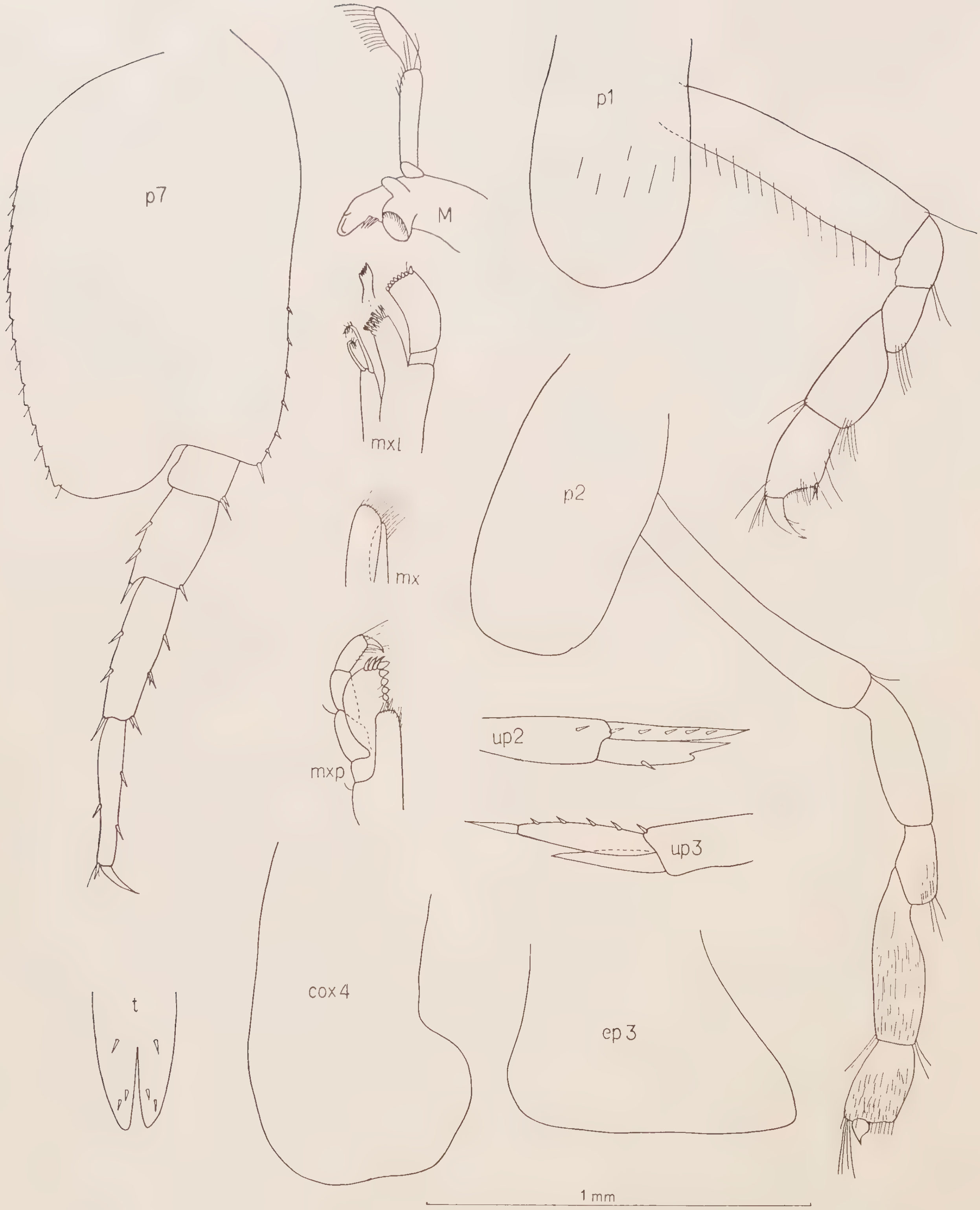


Fig. 9. *Tryphosa bruuni* n. sp.

Palp with first segment very short, third segment about two thirds of second.

Lobes of labium broad and short.

Maxillula with two terminal setae on inner plate, outer plate with 11 spines, proximal ones comb-like, distal ones with one single denticle. Palp with numerous short spines and one long spine near outer margin of distal end.

Inner plate of maxilla slightly shorter and distinctly narrower than outer plate.

Maxillipeds with outer plates almost semicircular, reaching just past second segment of palp, armed with three long, curved spines on distal margin, and with broad, laminar, obtuse teeth on inner margin. Inner plate with numerous terminal plumose spines, Last segment of palp well developed, unguiform.

First coxal plate hardly tapering distally. Posterior excavation of fourth coxal plate rather shallow, posterior angle obtuse. First gnathopod with basis long and carpus somewhat longer than metacarpus, palm oblique with two spines at posterior corner and a very fine but sharp crenulation, visible only with high magnification. Second gnathopod with basis long, carpus about twice the length of metacarpus, dactylus short and very rapidly tapering distally. Third and fourth pereiopods slender. Fifth to seventh pereiopods with basis broad and distal parts slender. First and third uropods reaching well past second uropod. End of first uropod level with tip of inner ramus of third uropod. First uropod with rami subequal, lanceolate, second uropod with outer ramus sligthly longer than inner and lanceolate, inner ramus abruptly constricted at about three fourths of its length and distal part narrow. Rami of third uropod narrow with inner ramus distinctly shorter than first segment of outer ramus.

It would perhaps have been better to refer the present species to a new genus. Its comparatively close relationship to *Tryphosa* is obvious, but its retention within the genus is not possible without violating the definition to a certain extent. Thus the epistome does not protrude past the labrum, the first segment of the accessory flagellum of the antennula is flattened and very long (as is often the case in deep-sea amphipods), the first coxal plate does not taper distally, the lobes of the telson lacks terminal spines, the inner ramus of the second uropod is abruptly constricted, and the inner ramus of the third uropod is distinctly shorter than the outer ramus.

These numerous discrepancies would, in themselves, well justify the creation of a now genus. When I refrain from following that course this is mainly because several other species of *Tryphosa* differ from the generic definition in one or more of the respects mentioned above, although as far as known at present not in all of them. Many species, however, are still badly known. I prefer to leave the question of a splitting up of the genus into new genera or subgenera to future investigators.

The species is dedicated to Dr. ANTON BRUUN, scientific leader of the "Galathea" Expedition.

Genus **Orchomenella** G. O. Sars

Orchomenella abyssorum (Stebbing)

St. 649. Kermadec Trench. 35°16'S 178°40' W, grey clay with pumice. 8210-8300 m. 14. II. 1952. 1 ♀, 12 mm.

The identity of this fine and well-preserved specimen with STEBBING's species from the "Challenger" collection is substantiated by a perfect agreement with respect to all features examined by me, e.g. the mouth parts, the pereiopoda, the uropoda. After examining it, however, I feel doubtful concerning the identity of this true *O. abyssorum* with the species recorded under that name from Antarctic waters by SCHELLENBERG (1926, p. 281) BARNARD (1932 p. 69), NICHOLLS (1938 p. 35), and myself (DAHL 1954 p. 282).

BARNARD (l. c.) first called attention to the peculiar armature of the palp of the maxillula which, in his fig. 28b is represented as having seven blunt teeth set more than their own width apart. Similarly NICHOLLS (lc.). states that "there are apparently 8 widespaced spine-teeth on one side, 7 on the other, flanked externally by one single seta." In the "Galathea" specimen the palp of the right maxillula has nine terminal teeth and one slender spine. The teeth are rather sharp and stand close together just as in STEBBING's drawing of the "Challenger" specimen.

Furthermore there is the question of the eyes. In the "Challenger" specimen STEBBING (1888 p. 677) states that they were "not clearly perceived, but probably large." This again agrees with the present specimen where no eyes can be definitely discerned but where the corresponding area is brownish and the cuticle looks different. In the Antarctic specimens the eyes are generally noted as distinct and brownish.

The matter is further complicated by some North Atlantic specimens also referred to the present species. In the specimen from the "Ingolf" collection mentioned by STEPHENSEN (1925 p. 125) the head was lacking. A number of further specimens, also from the North Atlantic, recorded by CHEVREUX (1935 p. 59) were neither described nor drawn. It appears not improbable that we have here at least two species, viz. one Antarctic species and one deep sea species, while the relationship of the North Atlantic form to either of these is at present unknown.

FAM. PHOXOCEPHALIDAE

Genus **Harpinia** Boeck

Harpinia spaercki n. sp.

St. 496. Banda Trench 5°36′S 131°06′ E, 7270 m, soft clay. Petersen Grab. 23. IX. 1951. 1 ♀.

St. 499. Banda Trench 5°21′S 131°17′E, 6580 m, greenish clay. Petersen Grab. 24. IX. 1951. 2 ♀♀ (types).

Description of female, 7 mm. Body smooth with only a few scattered and very fine hairs on dorsum of metasome. Hood reaching to end of antennular peduncle, its apex evenly rounded. No eyes. Postantennal corner of cephalon approximately rectangular, blunt. Epimeral plates without marginal setae, but one long plumose seta laterally on second epimeral plate. Posterior corner of third epimeral plate evenly rounded, posterior margin with one fine hair. Telson little longer than broad, cleft to base with lobes slightly diverging.

Basal segment of peduncle of antennula of about the same length as the two distal ones together and much broader. Ventral corner of distal margin with a group of four large plumose setae and various smaller ones. Second segment about twice the length of third segment, ventral corner of distal margin with a group of eight long non-plumose setae and six somewhat shorter ones, one of which is plumose. Distal margin of third segment with six setae of varying length. Flagellum with seven segments and accessory flagellum with six, accessory flagellum not much shorter than flagellum.

Peduncle of antenna with third segment slightly shorter than fourth and fifth segments and with a few setae near centre of ventral margin. Fourth segment widening distally with groups of numerous non-plumose setae on both upper and lower distal corner. Fifth segment with a row of non-plumose setae along larger part of ventral margin. Flagellum with six segments.

Maxilliped with inner plate reaching well past base of outer plate with tip truncate and armed with three setae and one spine. Of the setae the two more medial ones are distinctly plumose, the lateral one indistinctly so. The outer plate is long and narrow and reaches to the middle of the second segment of the palp. Palp slender with third segment but little shorter than second segment and about as long as dactylus.

Other mouth-parts not dissected.

First to fourth coxal plates with marginal setae, first plate somewhat broader distally, fourth plate with posterior incision not very large.

First and second gnathopods with merus and carpus subequal, metacarpus with palm oblique and posterior margin about as long as palm. Posterior corner of palm defined by a broad tooth and also by characteristically double-pointed spines of which there are two on first and one on second gnathopod.

Dactylus of third pereiopod much shorter than metacarpus, that of fourth pereiopod not much shorter than metacarpus. Fifth pereiopod with merus, carpus and dactylus about equally long, dactylus shorter. Sixth pereiopod with dactylus very long, subequal with metacarpus. Seventh periopod with posterior lobe of basis serrate but with small

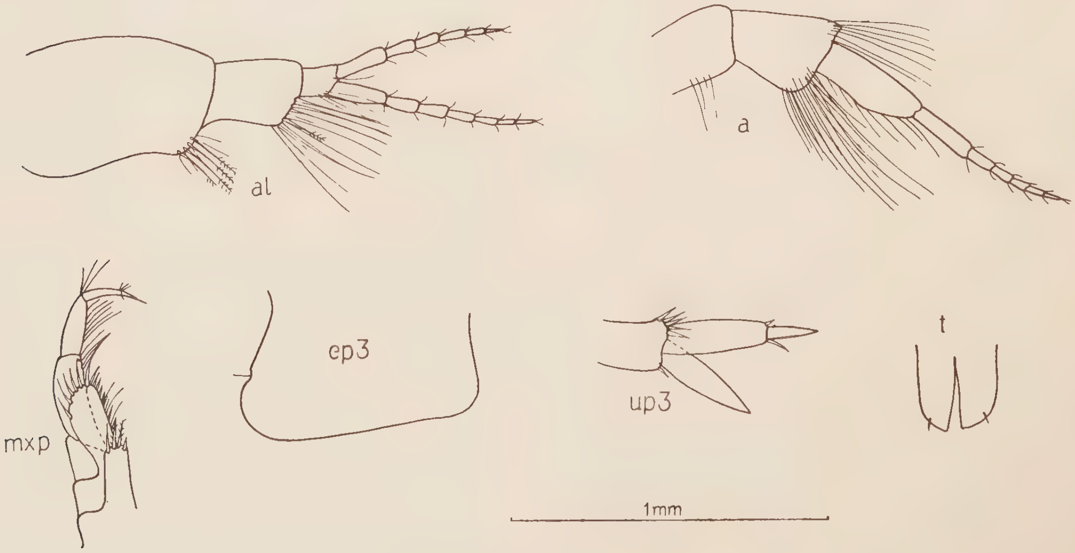


Fig. 10. *Harpinia spaercki* n. sp.

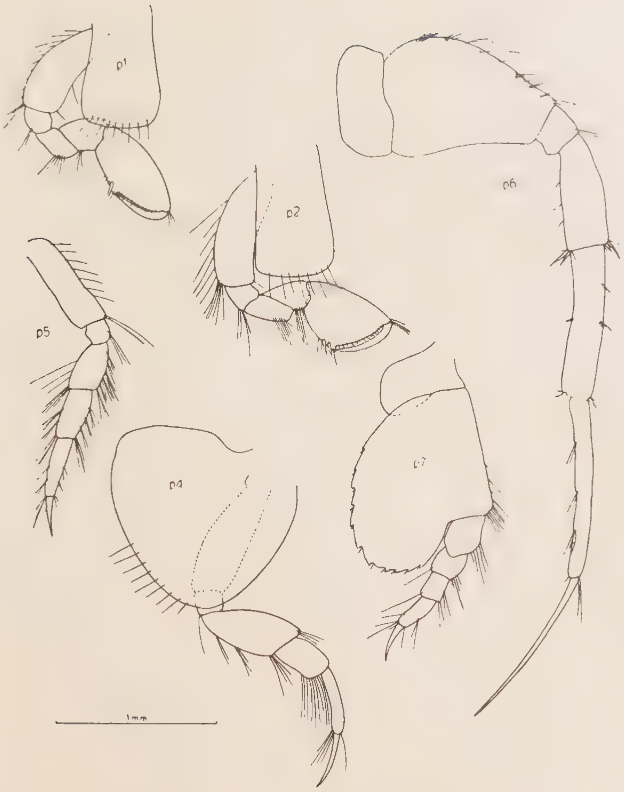


Fig. 11. *Harpinia spaercki* n. sp.

teeth and not particularly broad but very long, reaching almost to distal end of carpus.

Uropods with outer ramus longer than inner, peduncle of first uropod subequal with outer ramus, that of third uropod less than half as long as outer ramus. Inner ramus of third uropod reaching to end of first segment of outer ramus.

Pirlot (1932 p. 69ff.) described another species of *Harpinia* from fairly deep waters in the Sea of Timor and the Corontalo Golf, viz. *H. abyssalis* (a somewhat unfortunate name as it is likely to lead to confusion with the North Atlantic deep sea species *H. abyssi* G. O. Sars). It differs from *H. spaercki* in many respects and may be distinguished at the first glance by means of the third epimeral plate, the posterior corner of which is drawn out to form a long tooth. The posterior lobe of the basal segment of the seventh periopod is proportionally shorter and broader than in *H. spaercki,* and the dactylus of the sixth pereiopod is little more than half as long as the metacarpus. Besides those mentioned here there are also numerous other differences.

H. spaercki is also easily distinguished from the various North Atlantic and Antarctic deep sea species of *Harpinia.*

It should be noted that as long as the male of *H. spaercki* is not known it remains somewhat uncertain whether it is a true *Harpinia* or a *Harpiniopsis.*

The species is dedicated to Professor R. Spärck, Vice-President of the Committee of the "Galathea" Expedition.

FAMILY PARDALISCIDAE

Genus **Princaxelia** n. gen.

The amphipod species which was obtained in the greatest numbers in depths below 6000 meters belongs to the family Pardaliscidae, but its generic relationships caused certain difficulties.

In an appendix to his "Challenger" report Stebbing (1888, p. 1725) described the deep sea genus *Pardaliscoides* from the South Pacific. Further particulars, including numerous figures, of which there were none in the first description, were published in 1897 (p. 38 and pl. 12). Stephensen (1931 p. 217) in his "Ingolf" report referred three specimens captured SW of Iceland in a depth of 1505 m to Stebbing's *Pardaliscoides tenellus,* although with some hesitation. He stated, however, that his three specimens "upon the whole" conformed to Stebbing's description, which was founded upon one single female 8 mm in length. Stephensen added some points to the description and produced a series of highly relevant drawings.

Thanks to these drawings by Stephensen it is easy to see that the "Ingolf" and "Galathea" specimens belong to the same genus, and this was further confirmed by a re-examination of the "Ingolf" specimens which were kindly put at my disposal by Mr. Wolff.

On the other hand I find it impossible to agree with Stephensen concerning the identity of his species with *P. tenellus.* It is true that Stebbing's specimen was small and probably immature but on the other hand it differs from the "Ingolf" and "Galathea" specimens in various respects which should not be subject to relevant changes connected with sexual maturation. These points emerge from Stebbing's descriptions and drawings of 1888 and 1897, and his final diagnosis of the genus *Pardaliscoides* (1906 p. 224) seems to preclude the possibility of referring the present specimens to that genus. Stephensen's attitude was probably influenced by the bad state of preservation of his specimens. Now that numerous large and well-preserved specimens of both sexes are available the reasons for this cautious attitude have been removed.

The main points in which the present specimens differ from *Pardaliscoides* will be enumerated here.

The antennular peduncle of *Pardaliscoides* is not much shorter than the antennar peduncle. The second segment is longer than the first segment which, in its turn, is longer than the third segment. In the present specimens the antennular peduncle is short, much less than half the length of the antennar peduncle. Further its first segment is slightly longer than the second segment which is about twice the length of the third segment. In this respect the antennula very closely resembles that of *Pardalisca*.

The mandibles of *Pardaliscoides* have very few spines, 2 on the left and 3 on the right side, while in the present genus there are numerous slender spines, about 15 on each side, and moreover a group of 5-6 accessory spines. The palp of *Pardaliscoides* is slender with the middle segment half as long again as the distal segment. In the new genus the middle segment is expanded and subequal in length with the third segment.

In the maxillula the outer plate has more terminal spines and the palp is much broader in the new genus.

In the maxilliped of *Pardaliscoides* the outer plate does not reach the base of the second segment of the palp but in the new genus it does reach it.

The carpal segment of the gnathopods of the new genus is much more dilated and in the second uropod the rami are of equal length.

Some of the differences enumerated here may have little significance on the generic level, but those found in the structure of the antennulae and mandibles (spinulation and palp) are too great to permit the inclusion of the "Challenger", "Ingolf", and "Galathea" specimens under the same generic name.

The new genus, which will be defined below, is respectfully dedicated to H. R. H. Prince Axel, President of the "Galathea" Committee.

Princaxelia n. gen.

Urosome with dorsal teeth. Antennulae and antennae rather long, the antennulae being the longest. Flagella of both antennula and antenna with many segments. Accessory flagellum of antennula well developed. Right mandible with three blunt teeth on upper corner of cutting edge and no accessory plate, left mandible with less marked teeth but large and crenulate accessory plate. Both mandibles with a row of slender spines and a group of accessory spines. Maxillula, inner plate small with one terminal seta, outer plate with numerous (10) spines, the distal one much larger than the others, palp much expanded distally and with numerous spines on distal and inner margins. Maxilla, inner plate with 3 terminal setae, outer plate with numerous distal and lateral setae. Maxilliped with inner plates very small, outer plates likewise small, palp long and slender, dactylus large, with spinules. Carpus of first and second gnathopod much expanded and longer than metacarpus, third to seventh pereiopods slender, uropods with rami equal, first and second uropod with rami slender, third uropod with rami foliaceous. Telson long and narrow and deeply cleft.

It will be seen that the present genus in many respects, particularly in the structure of the antennula, and also that of the mandible and maxillula, is very similar to *Pardalisca*. On the other hand e. g. the maxilliped is so different that the two genera must be kept apart.

To *Princaxelia* as defined above two species must be referred, one from the North Atlantic collected by the "Ingolf" and one from the Pacific, collected by the "Galathea".

Princaxelia stephenseni n. sp.

Syn.: "? *Pardaliscoides tenellus* Stebbing". Stephensen (1931 p. 217).
non *P. tenellus* Stebbing (1888 p. 1725).

SW of Iceland: 60°37'N, 27°52'W, *1505 m*. 3 specimens (1 ♂ abt, 10 mm, paratype, 1 ♀ abt. 11 mm with large oostegites, type, anterior $^{2}/_{3}$ of another ♀ of approximately the same size). "Ingolf" St. 78.

For description and figures cf. Stephensen l. c.

To the description given by Stephensen the following additions should be made:

Cox 5-7 broad with more or less straight ventral margin. Posterior part deeper than anterior part. (Fig. 12 is drawn from the specimen dissected by Stephensen which should be the type of the species and the genus).

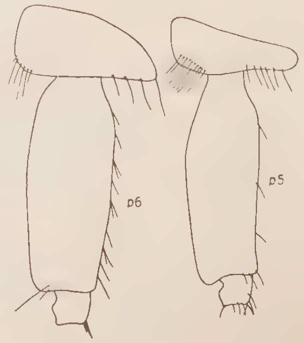


Fig. 12.
Princaxelia stephenseni
n. gen. et sp.

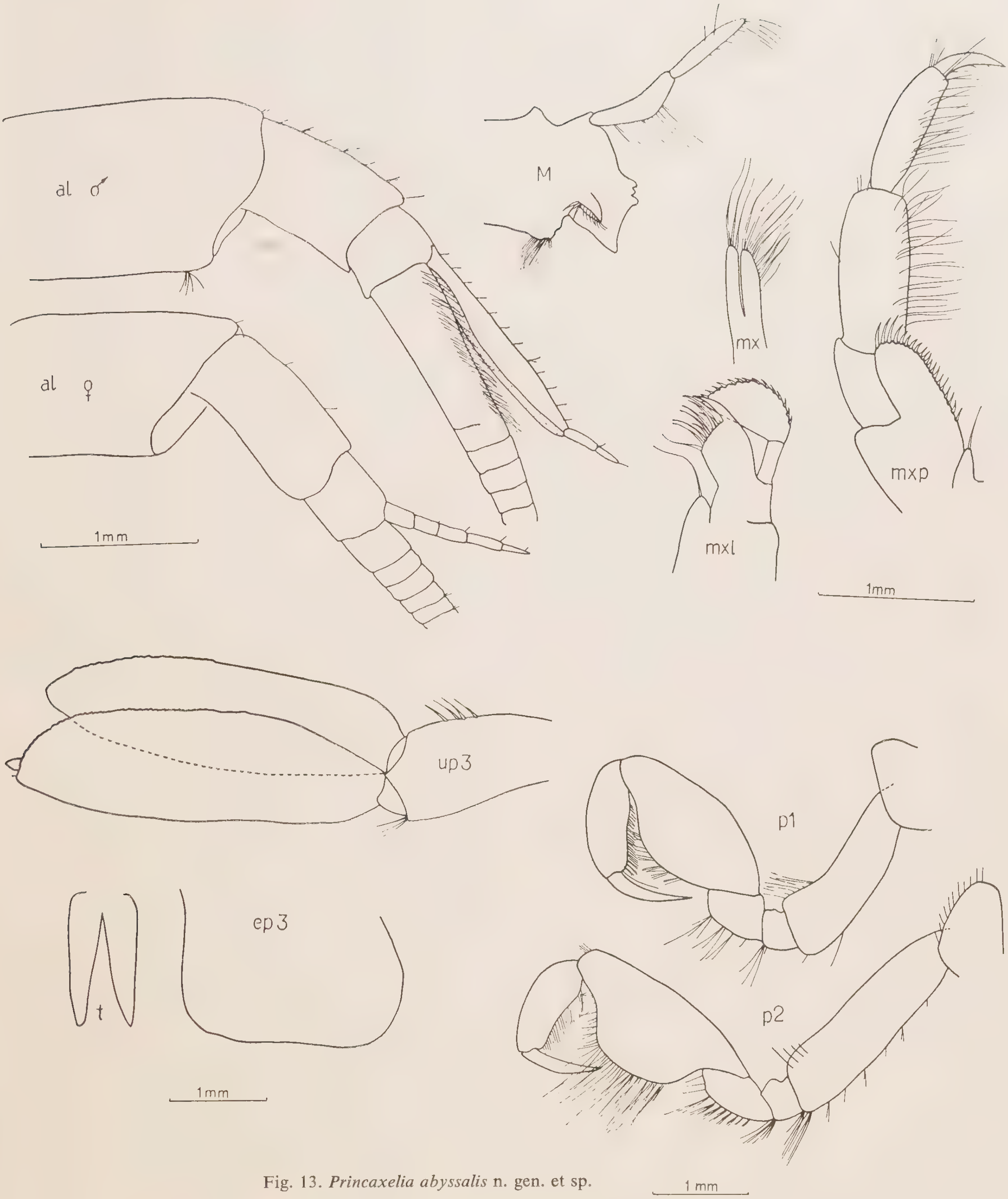


Fig. 13. *Princaxelia abyssalis* n. gen. et sp.

Princaxelia abyssalis n. sp.

St. 649. Kermadec Trench. 35°16′S 178°40′W, 8210-8300 m, grey clay with pumice. 14. II. 1952. 1 ♀, about 32 mm.

St. 650. Kermadec Trench. 32°20′S 176°54′W, 6620-6730 m, brown-grey clay with pumice. 15. II. 1952. 1 ♂, about 15 mm, urosome lacking.

St. 651. Kermadec Trench. 32°10′S 177°14′W, 6960-7000 m, 16. II. 1952. 1 ♀, 18 mm type, 1 ♂, about 21 mm paratype, 1 ♀ 11 mm, 1 sex?, badly mutilated.

Rostrum very short. Lateral lobes prominent, obtusely pointed. Two last urosome segments with dorsal denticle which points backwards as in *P. stephenseni*.

Dorsal margin of first and second urosome segments produced posteriorly to form a pointed tooth. Posterior angle of third epimeral plate rounded. Telson with lobes diverging with one small dorsal spine near base and one lateral spine about $^{1}/_{3}$ from base, one or two fine dorsal setae about $^{1}/_{4}$ from tip. Lobes terminally with small notch.

Antennula, accessory flagellum of ♀ with 5 segments (in type), 6 and 7 segments in large specimen from St. 649, that of male with two small segments besides large scale-like first segment. Fifth segment of antennar peduncle slightly shorter than fourth.

Mouth-parts as described in generic diagnosis, spine-row of mandible with about 15 slender spines and one group of 5-6 accessory spines.

First and second gnathopod with carpus very broad, especially that of second gnathopd. Metacarpus and dactylus subequal in length. Third and fourth pereiopoda with merus and carpus rather broad, carpus distinctly longer than merus.

Coxal plates of fifth to seventh pereiopod short but broad, with ventral margin straight or nearly straight. Distal part of appendages slender with basis not much broader than distal segments.

Up 1 and Up 2 with rami narrowly lanceolate, subequal, Up 3 with rami foliaceous, outer ramus slightly longer and with a small terminal process which represents second segment (Up 3 present only in large female from St. 649).

Undoubtedly *P. stephenseni* and *P. abyssalis* are closely related. The most striking difference is to be found in the palp of the maxillula which is very much expanded in *P. abyssalis* but hardly expanded at all in *P. stephenseni*. The number of spines in the spine-row of the mandible is also different, and so are the posterior coxal plates.

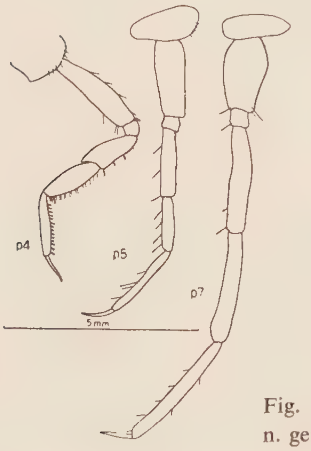


Fig. 14. *Princaxelia abyssalis* n. gen. et sp.

Genus **Pardaliscoides** Stebbing

Though *Hirondellea gigas* (cf. p. 214) was the only amphipod obtained in depths greater than 10.000 meters another species very nearly attained the same distinction. It is represented by a very small specimen captured in the Phillippine Trench at a depth of almost 10.000 m and was for a long time, also after the return of the expedition, considered to represent the depth record where amphipods were concerned. The specimens of *Hirondellea* were then considered to be bathypelagic, and although the possibility remains that they were actually caught above the bottom it seems very probable that they belong to a species which is at least facultatively benthic.

The present specimen which is only 4.5 mm long and apparently immature, was first taken to be a young specimen of the species described under the name of *Princaxelia abyssalis*. However, a re-examination disclosed the fact that it obviously belongs to the genus *Pardaliscoides*, described in an appendix to the "Challenger" report by STEBBING (1888 p. 1725) on a specimen captured at 39° S, 83° W. A more complete description with numerous figures was published later (STEBBING 1897 p. 38 and pl. 12).

Another specimen apparently belonging to the same species of similar size but rather badly mutilated in the anterior end was captured in the Kermadec Trench (St. 653).

As stated above the specimens captured by the "Galathea" conform very well with the generic description given by STEBBING, but it seems impossible to refer them to the same species. The third uropod is very different from the one of *P. tenellus* Stebbing, and the antennulary accessory flagellum of the specimen from the Phillippine Trench is proportionally much longer.

This last difference and some other discrepancies may be due to the apparently immature condition of the present specimens, but the shape of the third uropod appears sufficiently different to preclude any specific identity.

Pardaliscoides longicaudatus n sp.

St. 435, Philippine Trench, 10°20′N 126°41′E, 9820-10.000 m, very stiff clay. 7. VIII. 1951. 1 specimen 4.5 mm, immature (type).

St. 653. KermadecTrench, 32°09′S 176°35′W, 6180m, brown clay with pumice. 17. II. 1952. 1 spm., head mutilated, probably imm. about 4 mm.

Rostrum, distinct, curved downwards, not much shorter than first segment of antennular peduncle, Lateral lobes little produced, very obtusely pointed, Urosome segments 1 and 2 each with one pointed tooth on posterior dorsal margin. Posterior corner of third epimeral plate quadrangular but rounded at point.

Peduncle of antennula reaching just past end of fourth segment of antennar peduncle. In antennular peduncle the second segment is very distinctly the longest, while the first segment is not much longer than the third segment.

Only one antennula is left and its flagellum is broken, but it is nevertheless a good deal longer than the antenna. The accessory flagellum is notably long, it appears to be broken but the part left consists of 8 segments, the first of which is longer than the others. In the antenna the two ultimate peduncle segments are subequal, and together they are longer than the flagellum.

The mouth-parts were not dissected but in the mandibular palp the third segment is shorter than the second segment which is not dilated, and the maxilliped closely resembles that of *P. tenellus*.

First and second pereiopoda with carpus broad, third and fourth pereiopoda with merus and carpus not much broader than metacarpus. Coxa of fifth to seventh pereiopoda more or less rectangular and especially that of the fifth pereiopod rather large. Otherwise the three last pereiopoda are slender, but the basis of the seventh pereiopod is distinctly broader than those of the fifth and sixth pereiopoda. The dactyli of all pereiopoda are very long proportionally, but this may partly be due to the specimen being immature and not full-grown.

Uropods 1 and 2 reaching past uropod 3. Peduncle of Up 1 very long, subequal with inner ramus, outer ramus broken. Up 2 with rami unequal, peduncle shorter than rami. Up 3 with peduncle much shorter than rami, which are very long and slender, inner ramus very slightly longer than outer.

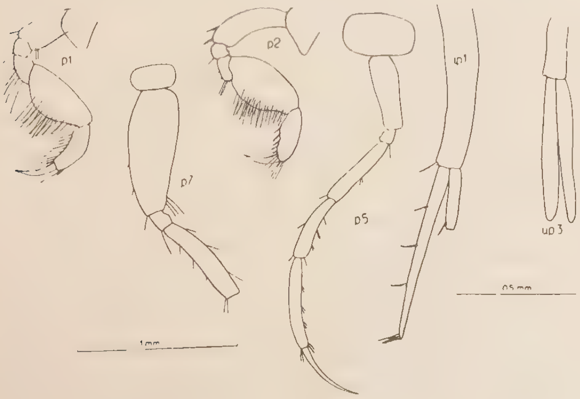


Fig. 15. *Pardaliscoides longicaudatus* n. sp.

It is somewhat doubtful whether the specimen from St. 653 really belongs to the same species. It is similar but in such a bad state that a definite identification is hardly possible.

Genus **Halice** Boeck

Syn. **Synopiodes** Stebbing

BIRSTEIN and VINOGRADOV (1955 p. 242) described two new species from the Kurile-Kamtchatka area which in their opinion obliterate the difference between the genera *Halice* and *Synopioides*, of which the former has the priority. They give a key to altogether nine species of *Halice*, including *H. aculeata* Chevreux and *H. secunda* (Stebbing). But according to SCHELLENBERG (1955 p. 190 and 194). *H. aculeata* Chevreux is identical with *Synopioides secundus* Stebbing, and as the latter specific name has priority this species should consequently be called *H. secunda* (Stebbing). Provisionally I accept SCHELLENBERG'S view.

Halice secunda (Stebbing)

Syn. **H. aculeata** Chevreux

Synopioides secundus Stebbing

St. 418. Philippine Trench, 10°13′N 126°43′E. 10.190-10.150 m, clay with gravel and stones. 21. VII. 1951. 1 ♂.

St. 651. Kermadec Trench, 32°10′S 177°14′W. 6960-7000 m, clay. 16. II. 1952. Anterior half of ♂.

It is practically certain that *H. secunda* is a purely pelagic species occurring in all three oceans. As it was obtained in two hauls where benthic species were also present, it is, however, mentioned her for the sake of completeness.

FAMILY EUSIRIIDAE

Genus **Rhachotropis** Smith

Rhachotropis flemmingi n. sp.

St. 466. Sunda Trench, 10°21′S 110°12′E. 7160 m. clay. 6. IX. 1951. 2 specimens 18-20 mm + fragments of at least 3 further specimens of about the same size or slightly larger.

Description of male, 18 mm.

No eyes. Rostrum long and slightly curved. Lateral lobes of cephalon produced, rounded. Postantennal corner not produced. Epistome somewhat produced, nearly straight.

One large dorsal tooth on the three metasome segments and the first urosome segment. Two posterior metasome segments and first urosome segment with distinct medial carina, lateral keels indistinct, but can be recognized at least on some segments. On the posterior margin of the three metasome segments the end of this indistinct, lateral keel is marked by a small tooth. Telson narrow, distal part tapering to a point, cleft for about one fifth of its length. Third epimeral plate with posterior corner broadly rounded, serrate.

Antennulae and antennae subequal, peduncle of both pairs compressed dorsoventrally with distinct lateral keel. First segment of antennar peduncle longer than second, third segment short. Antennar peduncle distinctly longer than antennular peduncle and fifth segment somewhat longer than fourth.

Left mandible with large molar, the edge of which is armed with a dense row of strong spines, spine-row with three large and some smaller spines, lacinia mobilis with six teeth, cutting edge with two teeth. Right mandible essentially similar but with cutting edge more produced. Maxillula, inner plate with two terminal setae, outer plate with 7 forked or indistinctly serrate spines. Palp with margins parallel, first segment about half as long as second segment. Maxilla normal with plates of equal length and inner plate broader than outer. Maxilliped with inner plate broad and armed distally with 4 short but heavy spines. Outer plate short, reaching just past first segment of palp.

Coxal plates small, first much produced anteriorly, subacute. Fourth coxal plate with small posterior emargination and posterior corner subacute. Fifth and sixth plates bilobate, posterior lobe larger than anterior lobe. Seventh coxal plate with distal margin straight.

Both gnathopods with palm very spinose, posterior end of palm marked by a group of heavier spines. Carpal lobe not reaching past posterior end of palm in either gnathopod.

Third and fourth pereiopods very slender with dactylus very long, equal with metacarpus. Fifth to seventh pereiopods also very long and slender, with posterior distal corner of merus somewhat produced and dactylus long. Posterior corner of basal lobe of fifth and sixth pereiopods rounded, that of seventh somewhat produced downwards and acute. Seventh pereiopod extremely elongate, approximately as long as whole body, and much longer than fifth and sixth pereiopods, which are subequal.

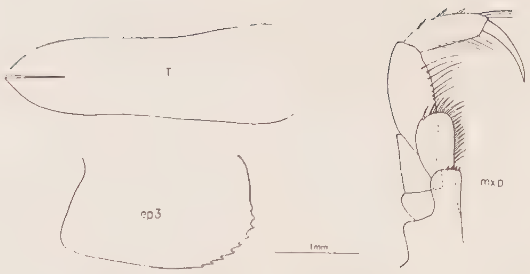


Fig. 16. *Rhachotropis flemmingi* n. sp.

First uropod reaching past second uropod and nearly to end of third uropod. Rami of first uropod subequal, outer ramus of second uropod slightly shorter than inner ramus. Third uropod with outer ramus very slightly shorter than inner ramus, both rami narrowly lanceolate, inner border of inner ramus with spine-row.

R. flemmingi may be defined as a blind species with metasome virtually unicarinate and with seventh pereiopod extremely long and with distal corner of basal lobe acute. Although these features, when taken separately, are known also from other species the combination is unique.

The species is dedicated to Count Flemming of Rosenborg, Naval Officer on board the "Galathea".

Eusiriidae, gen. et sp. ? (cf. **Rhachotropis).**

In the Kermadec Trench, St. 651, 7140-7180 m, a specimen was obtained which, although it undoubtedly belongs to the family Eusiriidae, is in such a fragmentary state that I prefer not to attempt to put any name to it.

The rostrum is small and bent downwards. The last metasome segment and the urosome are missing altogether. But on the badly mutilated first and second metasome segments a low carina ending in a rather small posterior tooth can be identified. Further the gnathopods are undoubtedly of the type found in *Rhachotropis* and closely resemble those described above in *R. flemmingi*. What remains of the other pereiopoda indicates that they were also long and slender. On the other hand the first coxal plate is not at all produced anteriorly, and there is no posterior lobe on the basal segment of the seventh pereiopod. In the maxilliped the outer plate reaches well past the first segment of the palp, and the second segment of the palp is rather broad in the middle and tapers both distally and proximally.

The specimen is a female with large óostegites

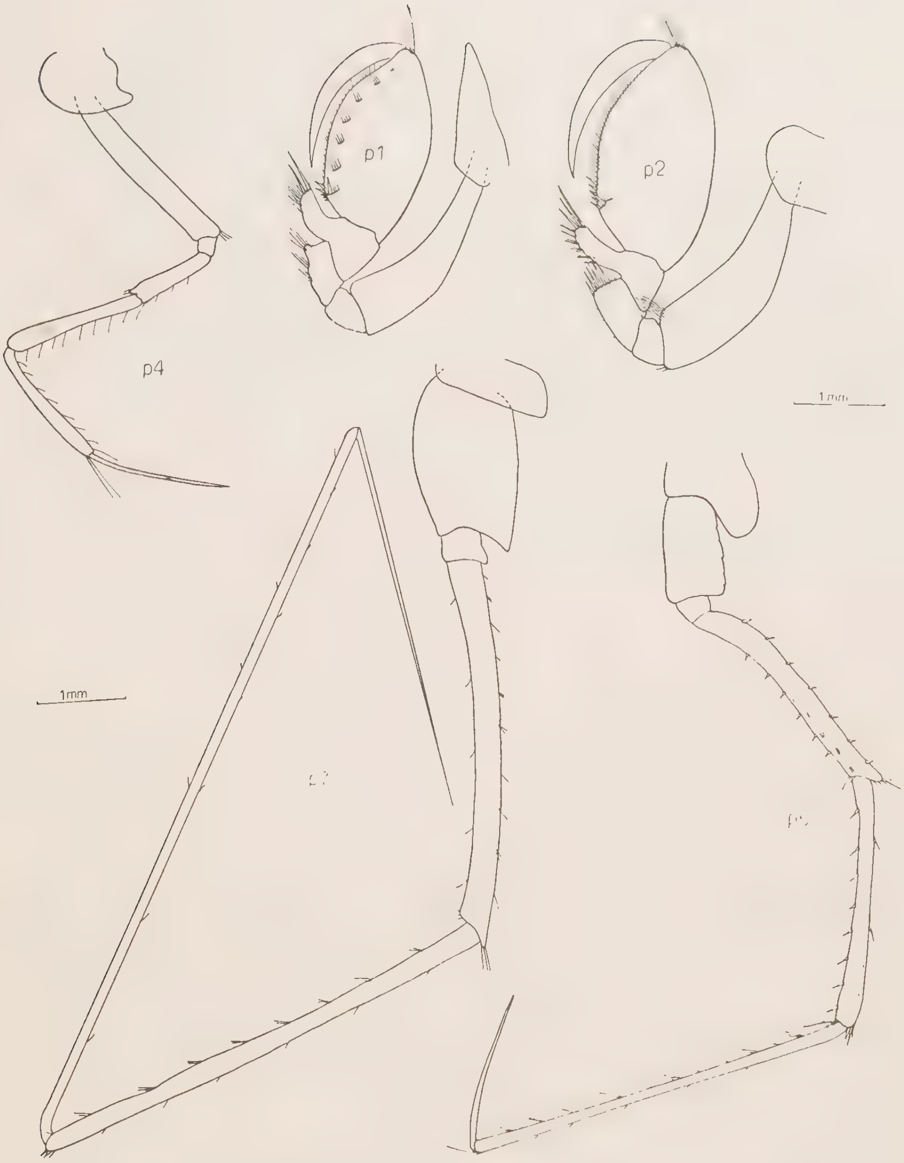


Fig. 17.
Rhachotropis flemmingi n. sp.

and must have measured between 15 and 20 mm in length.

It is above all the absence of the posterior part of the body with i. a. the third epimeral plate, the uropods, and the telson which make a definite identification impossible at the present stage. I have little doubt that the specimen represents a new species and it appears rather probable that a new genus must also be created for it when well-preserved specimens turn up.

FAMILY PONTOGENEIIDAE

Bathyschraderia n. gen. and allied genera

Among the rich crop of amphipods from the Kermadec Trench there are three very fine specimens and various fragments of a species which obviously belongs to the Pontogeneiidae. It is also clear that this new species belongs to a group of genera to which *Schraderia* Pfeffer and *Djerboa* Chevreux must also be counted.

The main characteristics of this group of genera could be summed up as follows: Both pairs of antennae long but antennula definitely longer than antenna, accessory flagellum present, both pairs of gnathopods very slender, especially the second pair, telson rather broad, with lobes truncate. Especially the gnathopoda distinguish these genera from all other members of the family at the first glance.

However close its relationships to the two other genera the new species cannot be referred to either of them.

To facilitate a comparison a number of important features have been plotted against each other in table 3.

Table 3

	Schraderia	*Djerboa*	*Bathyschraderia*
Eyes	present	present	absent
Dorsal spines on mesosome	absent	present	absent
Epistome, keel	absent	absent	present
Labrum, free margin	entire	entire	emarginate
Antennula, peduncle	segm. 1>2	segm. 1>2	segm. 1<2
Antenna, peduncle, length	normal	normal	very long
P 3-P 4 dactylus, convex side	unarmed	with strong spine	unarmed
P 5-P 7, dactylus, convex side	?	with strong spine	with numerous very slender spines
P 7 in relation to P 5 and P 6	slightly larger	very much larger	slightly larger
Mandible, distal segment of palp	truncate, setose terminally	normal, setose on inner margin	normal, setose on inner margin

Bathyschraderia n. gen.

Diagnosis: Rostrum small, slightly curved. No eyes. Cephalon longer than first body segment. Lateral lobes and postantennal corner broadly rounded, separated by a narrow slit. Body without dorsal teeth. Coxal plates rather deep, fourth excavate behind, fifth to seventh with posterior lobe little deeper than anterior lobe. Telson rather long and broad, rather deeply cleft. Antennula with peduncle rather long, second segment the longest, accessory flagellum small, antenna with peduncle very long, two ultimate segments subequal or ultimate segment slightly longer. Epistome with low keel, anterior margin of labrum emarginate. Mandibles powerful with lascinia mobilis on both sides, palp with two distal segments subequal, third segment distally narrowly rounded with setae on interior margin. Labium with accessory lobes obsolete. Maxillula with inner plate rather broad, numerous setae along inner margin. Maxilla with plates nearly equal, inner plate with transverse row of setae. Maxilliped with inner margin of outer plate lacking spines but bluntly serrate. Palp slender with second segment long.

Gnathopods subchelate and very slender, especially the second pair. Carpus and metacarpus with margins parallel. P 3 and P 4 slender. P 7 not notably larger than P 5 and P 6. Dactylus of P 5 to P 7 with spines on convex margin. Up 1 and 2 with rami slender, outer ramus shorter than inner, Up 3 with rami narrowly lanceolate, subequal.

Bathyschraderia magnifica n. sp.

St. 651. Kermadec Trench. 32°10'S 177°14'W. 6960-7000 m, brown clay with pumice. 16. II. 1952. 3 specimens + fragments.

Antennula with first segment of peduncle somewhat shorter than second segment, both with a small tooth-like projection on distal end of inner margin. Third segment of peduncle short, accessory flagellum with a number of terminal and subterminal setae. Antenna with peduncle distinctly longer than that of antennula, third segment of peduncle of antennula only reaching a little past fourth segment of antennar peduncle.

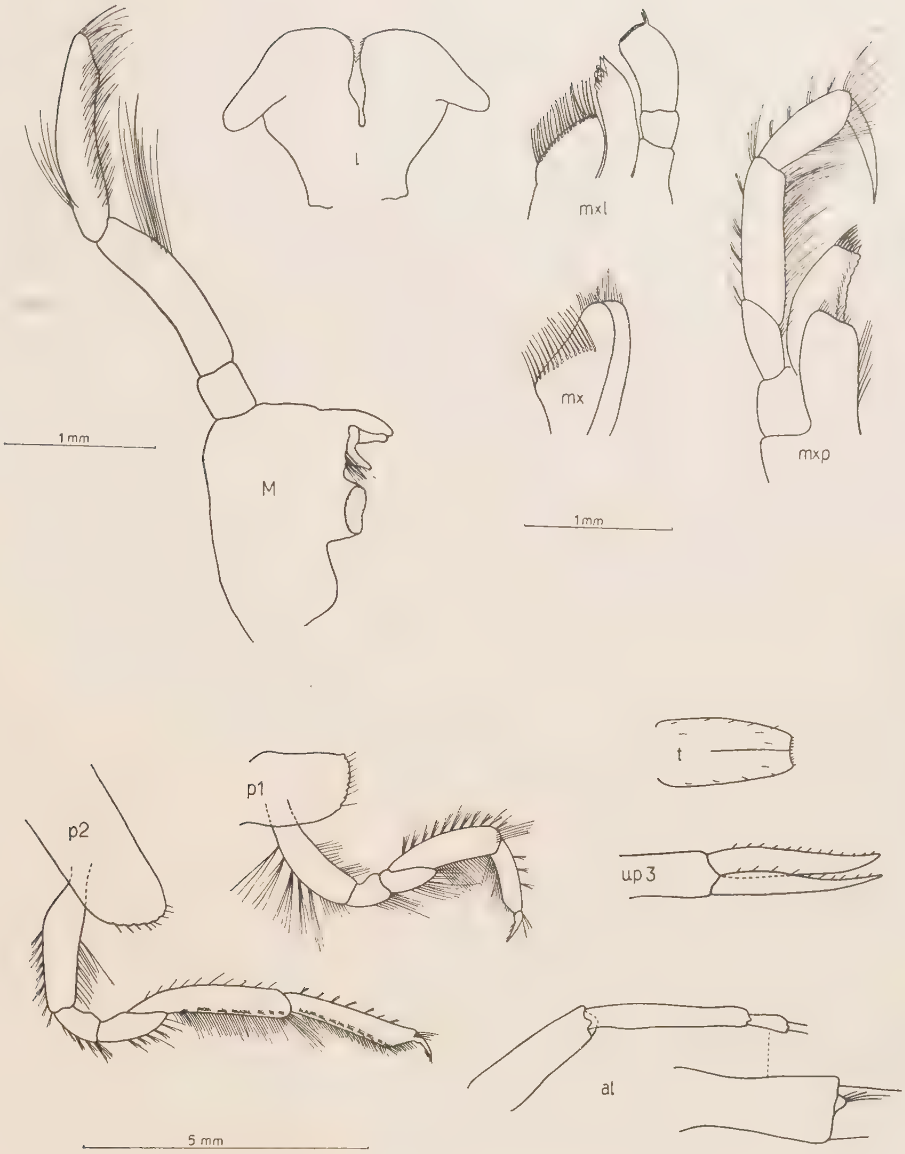
First to third coxal plates with distal margin rounded and bluntly serrate, fourth plate broad with distal margin straight.

P 1 and P 2 with palm very oblique and rather badly defined. Metacarpus of P 1 slightly shorter than carpus, those of P 2 subequal. P 3 and P 4 extremely slender, metacarpus of both appendages with a pair of rather large terminal spines. Hind lobe of basis on P 5 – P 7 with posterior margin nearly straight, distal margin projecting a little but not reaching distal end of ischia.

First epimeral plate with posterior corner nearly rectangular, posterior margin of second plate straight, corner slightly produced, posterior corner of third plate rounded with minute tooth.

First uropod with outer ramus slightly shorter than inner ramus, outer ramus of second uropod only two thirds the length of inner ramus, rami of

Fig. 18.
Bathyschraderia magnifica
n. gen. et sp.



third uropod subequal. Both rami of all uropods with row of spines on dorsal margin.

Telson with some dorsal spines. The number and arrangement appears to vary from specimen to specimen.

The slender appendages and general appearance of *B. magnifica* makes it rather probable that the species is pelagic or at least facultatively pelagic.

FAMILY LEPECHINELLIDAE

Genus **Lepechinella** Stebbing

Syn. **Dorbanella** Chevreux

The "Galathea" collection contains one very fine specimen of *Lepechinella* from the Kermadec Trench. With a total body length of between 15 and 20 mm it is by far the largest specimen of the genus hitherto recorded and of the same size as the related *Paralepechinella longipalpa* Pirlot.

The taxonomic position of *Lepechinella* caused some difficulties. Stebbing (1908) in his original description referred it to the Paramphithoidae, and as pointed out independently by Barnard (1925 p. 355) and Schellenberg (1926 p. 344) this was undoubtedly the reason why Chevreux (1914) referred the next species to be discovered to a new genus, *Dorbanella,* which he placed in the neighbourhood of the family Tironidae.

Schellenberg (1925 p. 205) maintained that the genus could have no very close affinity to the Tironidae, i. a. because of the different shape of the inner plates of both pairs of maxillae and the fusion of the two last urosome segments, and he created a new family Dorbanellidae to receive the genus *Dorbanella* Chevreux. Next year when he discovered the identity of the genus in question with *Lepechinella* Stebbing the name was duly changed to Lepechinellidae. In the same connection (1926 p. 344) he pointed out that it is impossible to follow Stebbing in referring the genus to the Paramphithoidae. Because of the fusion of the last urosome segments, the presence of well developed inner lobes on the labium, and the narrow basal segments of the pereiopoda the family Lepechinellidae should be ranged in the neigbourhood of the family Atylidae, a point of view which was later on accepted by BARNARD (1932 p. 186). PIRLOT (1933 p. 167) found it difficult to accept all previous views and suggested that the Lepechinellidae may constitute a branch of the family Gammaridae which has become highly specialized for life in the deep sea. He maintained that the fusion of the urosome segments is hardly any reason for placing the family in the neighbourhood of the Atylidae, and pointed out that e. g. among the hyperiids a fusion of the last urosome segments occurs frequently in various lines which are quite independent of each other.

On the whole the fusion of the last two urosome segments has come to play a central part in the discussion of the affinities of the Lepechinellidae. As the "Galathea" specimen throws some light upon this question some further remarks will be added.

STEBBING (1908) in his original description of the type species *L. chrysotheras* made no reference to any fusion of the two posterior urosome segments, but in his drawing they are represented as being separate as in ordinary amphipods. BARNARD (1925 p. 356) reported the occurrence of a species of *Lepechinella*, which, although it did not fit completely into the description given by STEBBING, was considered to be *L. chrysotheras*. The posterior urosome segments were stated to be separate. Later on BARNARD described a new species from the Antarctic, *L. cetrata*, (BARNARD 1932 pp. 186-187) where the last two urosome segments were found to be "united, but with the suture visible, at least laterally." A re-examination of the South-African *L. chrysotheras* disclosed the fact that despite the visible suture between the posterior urosome segments, they were nevertheless immovably united.

It is remarkable that despite the fact that a suture between the urosome segments was found in *L. chrysotheras* and later also in *L. cetrata* most writers on the family have taken the complete fusion of the segments in question for granted and considered it to be of great taxonomic importance. Such a complete fusion is found in *L. echinata* (Chevreux), *L. drygalskii* Schellenberg, *L. curvispina* Pirlot and in *Paralepechinella longipalpa* Pirlot. Probably the same is the case with *L. arctica* (Schellenberg). This species was first described as *Dorbanella sp.* (Schellenberg 1925 p. 206), and it was stated that the two posterior urosome segments were fused. Later on SCHELLENBERG (1926 p. 394 foot-note) gave it the specific name *L. arctica*. STEPHENSEN (1944 p. 19) re-described the species but had evidently overlooked SCHELLENBERG'S note and named it *L. schellenbergi*. In his drawing the two urosome segments are represented as fused without any trace of a suture. On the other hand the specimen drawn by GURJANOVA (1951 fig. 465 p. 677) as *L. arctica* Schellenberg has the two segments in question separated by a well-marked segmental border. In fact, however, other features, e. g. the epimeral plates and the coxal plates, differ so much from the drawing given by STEPHENSEN (1944 fig. 11 p. 19) that it seems doubtful whether the species are really identical. Finally the specimen taken by the "Galathea" not only shows a distinct segmental border between the two posterior urosome segments, a border which is clearly visible all around the body, but it was also found that they are slightly movable independently of one another.

Consequently among the Lepechinellidae a more or less distinct separation of the two last urosome segments was found in at least three species, viz.

L. chrysotheras Stebbing
L. cetrata Barnard
L. wolffi n. sp. (to be described below)

and possibly in two more, the South African *L. chrysotheras* (BARNARD 1925) and *L. arctica* sensu Gurjanova (1951) which may both be distinct species.

On the other hand a complete fusion seems to exist in five species, viz.

L. echinata (Chevreux)
L. drygalskii Schellenberg
L. arctica Schellenberg (s. str.)
L. curvispina Pirlot
Paralepechinella longipalpa Pirlot

Thus a tendency to fusion of the last two urosome segments may be said to exist within the family but it is by no means universal and does not play the important part suggested by various previous writers.

All this is not without a bearing upon the taxonomical position of the family. In the first place it adds weight to the argument advanced by PIRLOT (1933 p. 167) against the atylid affinities of the Lepechinellidae. The fusion of the posterior urosome segments constituted the main argument in favour of such affinities, as already pointed out by PIRLOT (1 .c.) most other features rather contradict it. It is highly improbable that atylids with the secondary fusion of the urosome segments characteristic of their family should have evolved in the direction of the lepechinellid type, at the same time gradually loosing that fusion. On the other hand, if the tendency to fusion of the urosome segments is now in the process of becoming established within the family, its members could hardly have been derived from atylids, which have already a fusion between the two segments.

The alternative suggested by PIRLOT, viz. that the Lepechinellidae are most closely related to the Gammaridae merits serious consideration. As mentioned above PIRLOT suggested that the Lepechinellidae might have evolved as a specialized deep sea branch of the latter family. *L. echinata* and *L. wolffi* have both been obtained in very deep water and the remaining species are in most cases recorded from depths a little above or below 1000 m. The mouth-parts of the Lepechinellidae are rather similar to those of the Gammaridae, the most important difference being the narrow inner plate of the maxillulae of the former family. Otherwise the resemblance with the Gammaridae is not particularly great. In fact it seems more fruitful to compare the Lepechinellidae with the Melphidippidae which are generally considered to be rather closely related to the Gammaridae.

In the Melphidippidae there exists a general tendency (also to be found in the Gammaridae) to develop strong spines on the dorsal side of the metasome and urosome segments the posterior margins of which are often crenelated. The basal segment of the three posterior pairs of pereiopoda is narrow, almost linear, and all the pereiopoda are long and very slender. The gnathopods are feebly subchelate with ill-defined posterior corner of the palm. The mouth parts closely resemble those of the Gammaridae. The two distal segments of the antennar peduncle are often very long. The rami of the uropoda are narrow. In all these respects the Melphidippidae resemble the Lepechinellidae. On the other hand the peduncle of the third uropod is always very long in the Melphidippidae and very short in the Lepechinellidae, and in the former family the dactylus in the two posterior pairs of pereiopoda is turned backwards. In contrast to the Lepechinellidae the Melphidippidae never have long dorsal spines on the anterior segments. Nevertheless the general resemblance between the Lepechinellidae and the Melphidippidae seems great enough to be more than accidental.

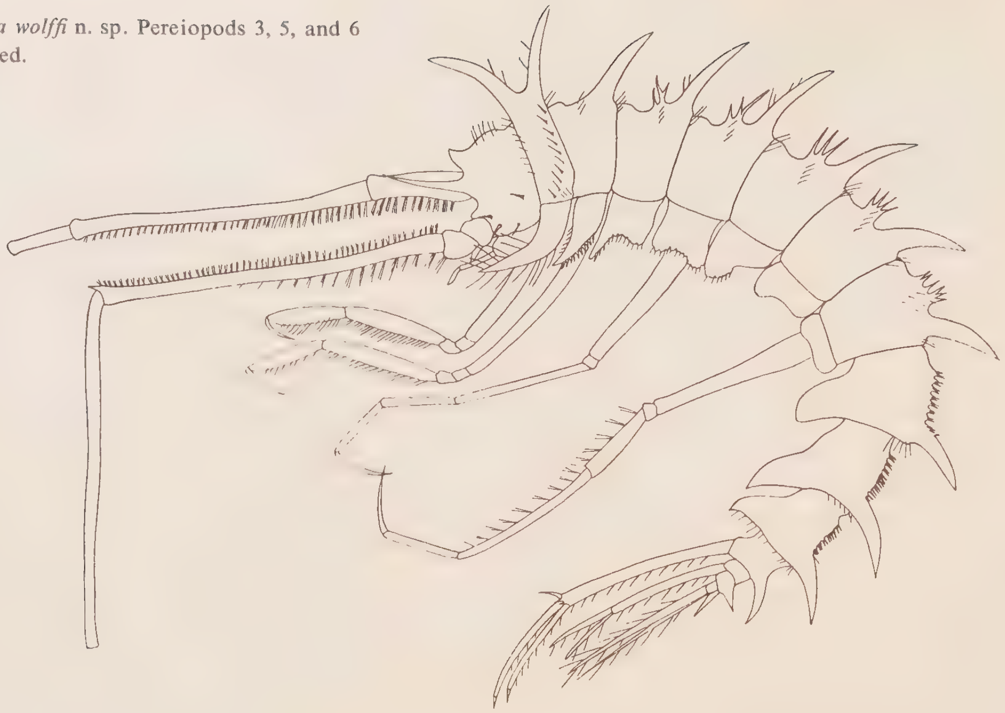
It would seem as if evidence is accumulating to support the opinion expressed by PIRLOT that the Lepechinellidae are not too far removed from the Gammaridae. At least it seems probable that they are more closely related to that family than to the others which have been mentioned in that connection. Particularly, however, there seems to be a considerable degree of similarity with the family Melphidippidae, and it seems to me that the Lepechinellidae are likely to find their definite place in the system in the neigbourhood of those two rather closely related families.

Lepechinella wolffi n. sp.

St. 658. Kermadec Trench, 35°51′S 178°31′W. 6660-6770 m, brown sand with clay and stones. 20. II. 1952. 1 female with large oostegites, 21 mm.

Body slender, very spinose. Rostrum short, curving upwards. Anterior margin of cephalon with two teeth, the upper one so long and acute that it could almost be called a spine, emanating at the height of the antennular base and only slightly shorter than the first segment of the antennular peduncle. Below it another much smaller and blunter tooth. Dorsum of cephalon with a group of small spines arranged in three rows. Other small spines on the sides of the cephalon. First free mesosome segment with two long dorsal teeth, the anterior one curving forwards, the posterior one curving backwards. Subsequent segments, including first segment of urosome, with one big tooth which curves slightly backwards. Second urosome segment without any dorsal tooth, third with a vertical, acute process. Besides the dorsal teeth there are large spines or groups of spines in front of the teeth on the five posterior mesosome segments. On the metasome segments the posterior part of the dorsum is provided with a rather high carina with a double row of spines, the big teeth are the posterior continuation of this carina. Hairs on posterior margins of segments.

Fig. 19. *Lepechinella wolffi* n. sp. Pereiopods 3, 5, and 6 and pleopods omitted.



Epimeral plates long with posterior margin straight or nearly straight, posterior corner of second and third plate somewhat produced.

Telson deeply cleft with lobes somewhat diverging.

Antennula with second segment of peduncle very long, flagellum long and slender, accessory flagellum short and rod-like, consisting of one segment only. Peduncle of antenna much longer than that of antennula, two distal segments subequal. Fourth segment ending in a small dorsal tooth. Flagellum of both sides lost.

Mandibular palp normal (i. e. similar to that of *L. curvispina, L. echinata,* and *L. chrysotheras)*. Other mouth parts of unique specimen not dissected.

First coxal plate long, curved and drawn out to a sharp point, along most of its length fringed by long hairs which sit well apart. Second coxal plate also ending in an acute point but hardly curved, provided with marginal spines. Third coxal plate with anterior corner produced into a sharp, straight tooth, posterior corner blunt. Fourth coxal plate bilobed with anterior and posterior lobes equal and blunt. Three posterior coxal plates with blunt anterior lobe which is obsolete in seventh coxal plate and posterior part of distal margin more or less straight.

All pereiopoda long and very slender, first two pairs feebly sub-chelate with palm badly defined, five posterior pairs with basis linear and dactylus very long.

First uropod long, reaching well past two posterior pairs. Peduncle longer than rami, ending in a big ventral spine. Dorsal margin of peduncle and rami with numerous spines. Rami subequal. Second uropod reaching to end of third, peduncle longer than rami, dorsal margin of peduncle and rami with numerous spines, rami subequal. Third uropod with peduncle very short, rami very slender, provided with numerous hairs and of about equal length.

L. wolffi belongs to the group of species within the genus *Lepechinella* which shows no cleaving of the first coxal plate, and where there are large dorsal teeth on the mesosome segments. This group consists of the species *L. curvispina, L. drygalskii,* and *L. echinata.* Of these three species *L. wolffi* undoubtedly resembles *L. echinata* most closely. An attempt to examine the species according to the key produced by STEPHENSEN (1944 p. 19) leads to *L. echinata.* From this species, however, *L. wolffi* is easily distinguished by the separation of the last urosome segments, the dorsal projection on the last urosome segment, and the subequal rami of the uropods. In *L. echinata* the posterior urosome segments are fused, the dorsal projection of the last segment is lacking, and the uropod rami are inequal.

The species is named after Dr. TORBEN WOLFF, First Scientist on the "Galathea".

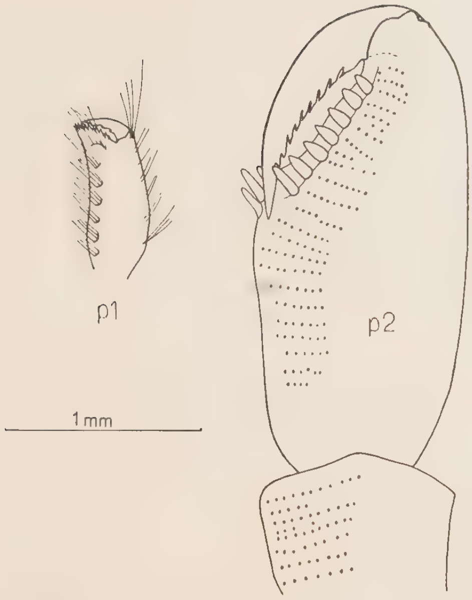


Fig. 20. *Bathyceradocus stephenseni* Pirlot. Setae on 2nd gnathopod omitted but their positions indicated by dots.

FAMILY GAMMARIDAE

Genus **Bathyceradocus** Pirlot

B. stephenseni Pirlot 1934

St. 495. Banda Trench. 5°26′S 130°58′E. 7290-7250 m, clay. 22. IX. 1951. 1 ♂, about 18 mm.

Unfortunately the very large specimen of this species, described by Pirlot (1934 p. 224 ff.) from the Moluccas Strait, is broken. Nevertheless the anterior fragment, consisting of the cephalon and the two anterior segments of the mesosome, fits the posterior fragment with the remaining segments so perfectly that there can be no doubt about their belonging to the same specimen. Pirlot had two females and one young specimen at his disposal, the present specimen is a male, and as the gnathopods differ substantially from those of the female, a drawing of them is reproduced here. The present specimen is about one and a half times as long as the largest one seen by Pirlot. Otherwise it conforms very well with the description.

THE DISTRIBUTION OF HADAL AMPHIPODS

Amphipods were obtained by the "Galathea" in the following four deep sea areas from depths of more than 6000 m, viz. the Sunda Trench, the Banda Trench, the Philippine Trench, and the Kermadec Trench. The various species mentioned in the taxonomic part of this paper were found to be distributed over the various hadal areas in the following manner:

The Banda Trench:

Onesimoides cavimanus Pirlot
Harpinia spaercki n. sp.
Bathyceradocus stephenseni Pirlot

The Sunda Trench:

Rhachotropis flemmingi n. sp.

The Philippine Trench:

Hirondellea gigas (Birstein & Vinogradov)
Pardaliscoides longicaudatus n. sp.
Halice secunda (Stebbing)

The Kermadec Trench:

Hirondellea dubia n. sp.
Schisturella galatheae n. sp.
Bathycallisoma pacifica n. sp.
Tryphosa bruuni n. sp.
Orchomenella abyssorum (Stebbing)
Princaxelia abyssalis n. sp.
? *Pardaliscoides longicaudatus* n. sp.
Bathyschraderia magnifica n. sp.
Halice secunda (Stebbing)
Lepechinella wolffi n. sp.

Besides the "Galathea" Expedition the Swedish Deep-Sea Expedition and the Russian expedition to the Kurile-Kamtchatka Trench also reported the occurrence of amphipods in depths of more than 6000 m.

Puerto Rico Trench (Schellenberg 1955)

aff. *Paracallisoma* sp. = Bathycallisoma schellenbergi Birstein & Vinogragov
Metandania islandica Stephensen
Eusirus bathybius Schellenberg
Halice secunda (Stebbing)

Kurile-Kamtchatka Trench (Birstein & Vinogradov 1955)
Hirondellea gigas Birstein & Vinogradov
Halice secunda (Stebbing) (recorded as *H. aculeata* Chevr.)
Vitjaziana gurjanovae Birstein & Vinogradov
Astyra bogorovi Birstein & Vinogradov
Cleonardo macrocephala Birstein & Vinogradov.

Thus no less than 21 species of Amphipoda Gammaridea have been recorded from depths exceeding 6000 m. It is interesting to note that although 10 different families have been recorded no less than

8 species belong to the family Lysianassidae, while the Pardaliscidae and the Eusiridae are both represented by 3 species. A complete list of the species in taxonomic order is composed as follows:

Fam. Lysianassidae
- *Hirondellea dubia* Kermadec Trench
- *Hirondellea gigas* Kurile-Kamtchatka Trench, Philippine Trench
- *Onesimoides cavimanus* Banda Trench
- *Schisturella galatheae* Kermadec Trench
- *Bathycallisoma pacifica* Kermadec Trench
- *B. schellenbergi* Puerto Rico Trench
- *Orchomenella abyssorum* Kermadec Trench, S. Atlantic, possibly cosmopolitic
- *Tryphosa bruuni* Kermadec Trench

Fam. Stegocephalidae
- *Metandania islandica* Puerto Rico Trench, N. Atlantic

Fam. Phoxocephalidae
- *Harpinia spaercki* Banda Trench

Fam. Pardaliscidae
- *Pardaliscoides longicaudatus* Philippine Trench, ? Kermadec Trench
- *Halice secunda* Philippine, Kermadec, Kurile-Kamtchatka and Puerto Rico Trenches + various other localities. Cosmopolitic.
- *Princaxelia abyssalis* Kermadec Trench

Fam. Vitjazianidae
- *Vitjaziana gurjanovae* Kurile-Kamtchatka Trench

Fam. Astyridae
- *Astyra bogonorovi* Kurile-Kamtchatka Trench

Fam. Eusiridae
- *Eusirus bathybius* Puerto Rico Trench
- *Rhachotropis flemmingi* Java Trench
- *Cleonardo macrocephala* Kurile-Kamtchatka Trench

Fam. Pontogeneiidae
- *Bathyschraderia magnifica* Kermadec Trench

Fam. Lepechinellidae
- *Lepechinella wolffi* Kermadec Trench

Fam. Gammaridae
- *Bathyceradocus stephenseni* Banda Trench.

The small number of species common to more than one of the deep sea trenches indicates a considerable degree of endemism. Only two of the species are definitely known to occur in more than one of the deep trenches, and both of those, *Hirondellea gigas* and *Halice secunda*, are known to be pelagic. *H. secunda* is most probably purely pelagic, while *H. gigas* may be facultatively so. This further underlines the important relationship between motility and geographical range to which I already called attention in 1954 (p. 47). For a more detailed discussion of these problems cf. Wolff (1956).

It should be pointed out that as far as the amphipods are concerned it is often extremely difficult to decide whether a species is to some extent pelagic. Closing trawls seem to provide the solution but so far the amphipods caught by this type of gear in the depths of the Atlantic by the Lamont Geological Station of the Columbia University have not been worked up.

With respect to the hadal areas investigated by the "Galathea" only one, the deep part of the Banda Trench, is situated in an area were the benthic amphipod fauna of somewhat shallower waters is comparatively well known. It is interesting to note that out of the three species of amphipods captured in more than 6000 m in the Banda Trench two had already been obtained by the "Siboga" Expedition. The working up of the amphipoda collected by the "Galathea" in depths between 2000 and 6000 m will probably throw some light upon the question of the bathymetric range of the benthic or mainly benthic hadal amphipods.

MORPHOLOGICAL ADAPTATIONS OF HADAL AMPHIPODS

Fairly extensive discussions of the morphological adaptations of deep sea amphipods were already published by Schellenberg (1926) and Pirlot (1936) and the "Galathea" collection from the deep trenches adds but little new information on this point.

All the species obtained by the "Galathea" in depths of more than 6000 m are apparently blind, which could be expected considering the great number of blind species among abyssal amphipods from less extreme depths.

Another interesting point should be mentioned. Pirlot (1936 p. 252) calls attention to the fact that among the deep sea species of the "Siboga"-expedition there are a group of species which are supposed to occur on the surface of the deep sea mud. He points out that the most striking characteristics of this group of species is their long and slender bodies which are often provided with dorsal projections, and, above all, their very long and very slender appendages. As typical representatives of this type he mentions *Lepechinella curvispinosa*, *Paralepechinella longipalpa*, and *Rachotropis sibogae*. It is interesting to note that some of the new species described here, and notably *Lepechinella wolffi* and *Rachotropis flemmingi*, are even more extreme in this respect than the closely related species dealt with by PIRLOT.

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VAMPYROMORPHA

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INTRODUCTION

Fifteen specimens of *Vampyroteuthis infernalis* Chun were captured by the Danish Deep-Sea (Galathea) Expedition (Table 1). The collection includes an exceptionally large and moderately well preserved sexually mature female from off Durban, South Africa. This unusual animal is described in detail below. Comparison with previous data (PICKFORD, 1948) shows that it does not differ significantly, except in size, from smaller adults of the same sex. The other specimens, with the exception of two immature adult females, are more or less severely damaged and descriptions have been limited to essential features and points of controversial interest.

In the descriptions which follow the specimens are numbered 105-119, in continuation of the author's list of known representatives of this unique cephalopod. Specimens 1-77 were described previously in the Dana-Reports (PICKFORD, 1946, 1948); specimens 78-95 were collected by the Bermuda Oceanographic Expeditions (PICKFORD, 1950) and specimens 96-104 were collected by the Discovery Expeditions (PICKFORD, 1952). There is an undescribed specimen in the Zoological Museum at Copenhagen, collected by the Atlantide (Stn. 139) and identified by Dr. ANTON F. BRUUN. It is a Stage 2 larva measuring 11 mm. in mantle length and is listed in the author's catalogue as specimen 120.

The author wishes to take this opportunity of expressing her thanks to Dr. ANTON F. BRUUN and the Committee of the Galathea Expedition for the privilege of participating in the work of the expedition during three months, while collections were being made in the Indian Ocean, Gulf of Siam, and South China Sea. Dr. TORBEN WOLFF kindly made notes on the natural color of some specimens that were captured at a later date.

DESCRIPTION OF THE SPECIMENS

Specimen 105

This remarkable specimen, taken off Durban, is a sexually mature female that had recently spawned. One egg can be seen in the coelom, and another distorted egg was found in the preserving fluid. The external surface is badly rubbed, the arm tips are damaged, and most of the suckers are lost. The oral face of the web, examined two months after preservation in neutral sea-water formalin, was still black. The right eye is damaged and the lens gone, the left eye is missing.

The standard measurements are given in Table 2, and the corresponding indices are listed in comparison with the range and mean for previously described Stage 5 females. The mantle length is approximately 100 mm. This is about 25 % greater than the estimated mantle length for the largest previously described specimen. The latter (Specimen 1; PICKFORD, 1946, 1948) was taken by the Dana Expedition in the Gulf of Panama and is also a sexually mature female. Its apparent mantle length, 63 mm., was undoubtedly shorter than natural

Table 1. List of specimens of *Vampyroteuthis infernalis* Chun taken by the Danish Deep-Sea Expedition

Spec. No.[1]	Stn	Locality	Latitude	Longitude	Date	Depth m.	EFD m.[2]	Stage and Sex
105	190	Off Durban	29°42′S	33°19′E	3.II.51	2720	–	Mature ♀
106	–	–	–	–	–	–	–	Mature ♂
107	279	Seychelles to Ceylon	1°00′N	76°17′E	8.IV.51	4320	–	Fragments of young adult, ? sex.
108	301	Bay of Bengal	19°30′N	86°32′E	25.IV.51	1110	700–800	Stage 4 larva, ? sex.
109	–	–	–	–	–	–	–	Adult, ? sex.
110	314	–	15°54′N	90°17′E	3.V.51	2600	–	Adult ♂
111	318	–	9°02′N	93°07′E	5.V.51	1440	800–1100	Adult ♂
112	–	–	–	–	–	–	–	Adult, ? sex.
113	471	Sunda Trench	10°26′S	114°15′E	10.IX.51	2990–2810	–	Stage 3 larva, ? sex
114	472	–	10°24′S	114°07′E	10.IX.51	2250–2030	–	Stage 4 larva, ? ♀
115	–	–	–	–	–	–	–	–
116	–	–	–	–	–	–	–	–
117	–	–	–	–	–	–	–	Eye of larva, prob. Stage 4.
118	601	Tasman Sea	45°51′S	164°32′E	14.I.52	4400	–	Immature Stage 5 ♀
119	660	Kermadec Trench	35°35′S	178°51′W	22.II.52	7800–7310	–	Immature Stage 5 ♀

1. Author's list, see text.
2. Estimated Fishing Depth, given only for pelagic hauls.

owing to strong contraction of the mantle, and an estimated true mantle length of ca. 76 mm. was suggested. The mantle-width index of Specimen 105 is at the lowest limit for Stage 5 females. Head width could not be measured accurately on account of the damaged condition of the remaining right eye, but it was estimated by doubling the distance from the center of the head to the outer limit of the lensless right eye. The head-width index, based on this measurement, is at the lowest limit for Stage 5 females.

The anterior fin-length index is normal, but the fin is unusually narrow. This is certainly due, in part, to rubbing of the delicate fin margin. The fin-base index is normal.

The first right arm has a regenerated tip, and the extremities of the fourth right and first, second and fourth left arms are damaged, precluding accurate measurement. Of the remaining arms, the third left is longest, measuring 200 mm., while the second and third right arms measure 190 mm. The total length of the animal is approximately 285 mm. and, on the assumption that the third left arm was actually longest (or subequal to the longest), the arm-length index is 70. This is somewhat greater than the highest hitherto recorded but, on account of the positive growth coefficient for arm length in relation to mantle length, it was predicted that the arms of larger animals would be relatively longer than those of smaller specimens (Pickford, 1948). The state of preservation does not permit comparison of the order of arm length, but the arms are evidently subequal; previous data indicated that the first and second arms tended to be longer than the third and fourth, although the differences are not great and there are many exceptions.

Measurements of web depth are as follows: sector A, 104 mm.; left sector B, 84 mm.; right sector B, 82 mm.; left sector C, 77 mm.; right sector C not sufficiently well preserved for measurement; left sector D, 62 mm.; right sector D not sufficiently well preserved for measurement; sector E, 96 mm. The order of web depth is therefore A:E:B:C:D. In other specimens, as in this, the A sector is usually the deepest, but the E sector is most frequently the shallowest. However, the measurement varies greatly with the state of contraction and distortion, so that no special significance can be attached to the greater depth of the E sector in Specimen 105. The web-depth index, and the disparity index between shallowest and deepest sectors, are normal.

The diameter of the largest sucker provides a normal sucker-diameter index. No arms bear a complete set of suckers: none are preserved on the left arms, there are three on the first right arm, seven on the second right, and none on the third and fourth right arms. A specimen of this size would be expected, from previous calculations, to have about 35 suckers on a perfect arm.

The cirri are unusually long and attenuated, perhaps as a result of the conditions of capture and preservation; the cirrus-length index of 15 is well

Table 2. Measurements and indices of Specimen 105, compared with previously described Stage 5 females.

Character	Measurement mm.	Index[1]	Range and *mean* for previously described specimens[2]
Total length	285	–	180[3]
Mantle length	100	–	55,63[3]
Mantle width	60	60	60-**75**-102
Head width	82	82	80-**95**-109
Anterior fin:			
Length	57	57	33-**53**-69
Width	20	32.5	44-**50**-68
Base	18	31.6	26-**38**-58
Longest arm	200	70	51-**61**-68
Sucker diameter	3.6	3.6	2.0-**3·0**-4.8
Cirrus length	15	15	6.9-**9·1**-10.9
Web depth:			
Deepest	104	52	43-**61**-72
Shallowest	62	57.5	43-**63**-92
Eye diameter	29	29	29-**39**-48
Fin light organ:			
Length	4.0	4.0	3.9-**5·2**-6.9
Width	3.6	90	66-**88**-100
Composite light organ:			
Length	4.2	4.2	5.1-**6·7**-9.1
Width	2.5	60	31-**45**-65
Number of nodules	ca. 30	–	38-**54**-76
Gill length	25	25	19-**23**-28
Number of primary gill lamellae per demibranch	11,12	–	10-**12**-15
Funnel length	31	31	36-**41**-47
Lower jaw:			
Rostral length	16	16	12-**14**-17
Rostral notch	5.5	34.5	34-**41**-46
Gladius:			
Length	96	–	65 and (?) 76.2[3]
Inner asymptote length[4]	77	80.2	66-**75**-83
Outer asymptote length[4]	60	78	62-**72**-81
Pro-ostracal breadth	25	26	18-**23**-27
Lateral plate breadth	38	39.6	32-**38**-44
Conus vane:			
Breadth	37	38.5	31-**36**-45
Depth	19	19.8	14-**18**-22

1. Definition of indices and previous data from Pickford (1948).
2. Indices or numerical value if so indicated.
3. Measurement in mm. for two previously described mature females.
4. Measured from apex of conus, without rostrum.

above the range for Stage 5 females and, with one doubtful exception (Specimen 28; Pickford, 1948), no such high values have been recorded for younger stages. The number of primary cirrus pairs could be counted on some of the arms since, even when the first sucker is missing, its torn stump can be seen. The first arms have 7 pairs, the second right 7 pairs, the third left 6 pairs; the fourth arms also probably had only 6 pairs, although this is not certain. However, the specimen evidently conforms to the pattern for Indo-Pacific *Vampyroteuthis*, discussed in the next section; in these oceans the typical maximum number of primary cirrus pairs is 7, the typical minimum number 5.

The diameter of the damaged right eye is somewhat uncertain on account of its collapsed condition. The estimated diameter gives an eye-diameter index which is at the lowest limit of the range for Stage 5 females. The lens is not preserved, but a rough estimate based on the diameter of the lensless pupil aperture suggests that it may have been about 9 mm. Previous calculations indicate that this would be about right for an eye of this size.

The fin light organs are preserved; the length-width index is normal but the size, in terms of mantle length (fin light organ-length index) is low, at the lowest limit for Stage 5 females. The left composite light organ is better preserved than the right and was therefore selected for study. The shape, reflected in the width-length index, is normal, but the relative size in terms of mantle length is unusually small. The small size of the organ is also apparently reflected in the small number of luminescent nodules; only about 30 could be counted, as compared with normal counts of 38-76 in Stage 5 females (mean 54). It was thought, from previous data (Pickford, 1948), that the composite light organs were significantly larger in females than in males, but, in the case of Specimen 105, the length index is at the lowest limit even for Stage 5 males. The hypothesis of a sex difference, which is reviewed in the next section, may have to be abandoned but, at the present time, it seems more probable that Specimen 105 is aberrant.

The gills are well preserved and the relative length, reflected in the gill-length index, is normal. There are 11 primary lamellae in the outer and 12 in the inner demibranch, making a total of 24 if the terminal lamella is included. This is normal for adults of either sex. The hypothesis that no new gill lamellae are added after metamorphosis receives welcome confirmation from so large an animal.

The funnel is rather short, with a funnel-length index of only 31; similar figures have been recorded for males but there are no grounds for suspecting that there is a sexual difference and presumably the low value in Specimen 105 can be attributed to the state of contraction.

The jaws were studied *in situ* since it was not desired to damage the specimen by removal of the buccal mass. Only two measurements could be made, the rostral length and rostral notch length of the lower jaw. The rostral-length index is near maximal for Stage 5 females. Previous studies suggested that the jaws of adult females were relatively larger than those of males, and the rostral-length index of Specimen 105 supports this hypothesis. However, two immature Stage 5 females (see below) were low. The rostral notch of Specimen 105 is rather short, but the index is in the range for previously described specimens.

The diameter of the single coelomic egg is 4 mm., in good agreement with previous findings which indicated an average diameter of 3.86 mm for free eggs attributed to this species (PICKFORD, 1949). The diameter of the sucker-like oviducal aperture is 9 mm., which is very large. In the case of the two previously described adult females the diameters were 3.2 mm. and ca. 5.5 mm. respectively. In terms of actual (not corrected) mantle length these figures give indices of 9, 5.8 and 8.7 respectively.

The gladius was removed and studied in detail. The total length of 96 mm. is greater than anticipated from previous data regarding the relationship between gladius length and mantle length. Calculations based on equations for all stages (PICKFORD, 1948) indicated that a specimen of 100 mm. mantle length would have a gladius of about 87 mm. It should be noted that one other very large female (Specimen 2; PICKFORD, 1948) had a gladius length that was also considerably longer than anticipated (mantle length 55 mm., gladius length 65 mm.). These differences may be incidental to the inaccuracies of exact mantle length measurement, but it is possible that a different allometric equation should be applied to mature females. The proportions of the gladius, reflected in a series of indices given in Table 2, are normal for Stage 5 females. The only feature of interest was the presence of a well developed rostrum, an apical projection that is sometimes, but not always, present in the vampyromorph gladius; an example was figured previously (PICKFORD, 1948, Fig. 41).

As a general conclusion, it can be stated that Specimen 105 is an unusually large but otherwise typical female of *Vampyroteuthis infernalis* Chun.

Specimen 106

This sexually mature male was taken off Durban, South Africa, in the same haul as the sexually mature female described above. It is badly rubbed and a great deal of mud is entangled in the skin and on the exposed underlying tissues. The color, after five years preservation in neutral sea water formalin, is completely faded. A tangled mass of skin at the apex makes an exact measurement of mantle length uncertain, but an approximate estimate of 46 mm. is probably correct. Calculations from the rostral length of the lower jaw, which measures 5.5 mm., would give an expected mantle length of 43.9 mm. The size is therefore in agreement with the mean of 49.2 mm. based on four previously captured sexually mature males (range 44-55 mm.). This finding tends to confirm the hypothesis that adult males are considerably smaller than adult females, but a mature male described below (Specimen 110) was somewhat larger.

The mantle width, which was ca. 34 mm., could only be measured approximately. The head width, ca. 31 mm., is also uncertain since both eyes are damaged. The corresponding indices for mantle-width and head-width are 74 and 67.5 respectively; the former is in the expected range for adult males, but the latter is unusually narrow.

The fins are in good condition, except for rubbing of the skin. Measurements are the same for right and left sides: length 32.5 mm., maximum breadth 13 mm., width of fin base 10 mm. The fin-length index, 70.7, is higher than previous records for Stage 5 males, but no great significance can be attached to this owing to the uncertainty as to the true mantle length. One Stage 5 female had an index of 69. The fin-width index is unusually narrow, 40.0, probably owing to rubbing of the skin. The fin-base index is also unusually narrow, 30.8, presumably for the same reason.

The arm crown is badly damaged; the longest arm (third left) measures 120 mm. It is complete but badly rubbed and apparently attenuated. The approximate total length of the animal is ca. 160 mm, giving an arm-length index of 75 which is in the normal range, but high. The suckers and cirri are not preserved and the web depth could not be studied.

The eyes are collapsed and distorted, but the eye diameter was probably about 14 mm. This gives an eye-diameter index of 30.5 which is rather low. The diameter of the somewhat damaged left lens is about 6 mm., giving a lens-diameter index of 42.8, which is normal for adults of both sexes.

The light organs are not preserved, and the gills are too badly rubbed for study. The rostral length of the lower jaw is 5.5 mm. giving a rostral-length index of 12, which is normal for adult males, thus tending to confirm the hypothesis that males have smaller jaws than females. The rostral notch measures 2 mm. and the rostral-notch index, 36.4, is rather low for Stage 5 males. The gladius was not studied.

Specimen 107

This example, taken between the Seychelles and Ceylon, consists of five fragments of a medium sized specimen, preserved in alcohol. Apparently all parts belonged to the same specimen and the following observations on the fragments may be noted:

1. Part of the arm crown with the posterior salivary glands attached. The oral face of the web was black, two weeks after capture.
2. The rest of the arm crown.
3. The buccal mass. Length of lower jaw 6 mm., rostral length 5 mm., length of rostral notch 1.6 mm. The estimated mantle length, calculated from the rostral length, is 37 mm. The rostral notch index, 32, is rather low.
4. The brain with optic lobes and eyes; the whole length of the oesophagus attached.
5. Parts of the visceral mass with the gills. The gill length is ca. 6.2 mm., and the estimated mantle length, calculated from the gill length, would be about 33 mm. This is in reasonable agreement with the estimate of 37 mm. derived from the lower jaw.

The sex could not be determined and the fins are not preserved. However, the estimated mantle length suggests that the specimen was a young individual that had just completed metamorphosis. It is larger than any recorded Stage 4 specimen, and within the minimum for Stage 5.

Specimens 108 and 109

The damaged remains of two specimens were taken at Stn 301, in the Bay of Bengal. The better preserved example, Specimen 108, was found entangled in the net and, in consequence, it is severely damaged. The oral face of the web, when freshly caught, was black. The sex is presumably female, since no remains of male organs could be discovered. The mantle length of 22.5 mm. indicates that it was a larva, probably in Stage 4. However, no signs of the posterior fins could be discovered, which suggests that they may have been in the last stages of resorption and, in view of the poor condition of the specimen, their apparent absence is not significant. The size agrees with the mean for Stage 4 larvae, and is far below that of any metamorphosed Stage 5 specimen. The head width, ca. 24 mm., gives a head-width index of 107, which is in the high range but not unusual. The left anterior fin measures 9 mm., which is larger than would be expected in an animal of this size. The calculated mantle length, derived from the allometric equation for larvae in Stages 2-3, would be 26.7 mm. for an animal with the fin length of this specimen.

Specimen 109 consists of two damaged fragments that apparently belong to the same animal. One piece consists of an arm and web, the other an arm fragment. Both arms have suckers with a maximum diameter of 2.1 mm.; this would correspond to an estimated mantle length of 57 mm., derived from the allometric equation for Stage 5 specimens. The animal may therefore have been an adult male, or an immature Stage 5 female.

Specimen 110

This specimen, a male from Stn 314 in the Bay of Bengal, is in poor condition. The mantle skin and fins are torn away from the shell sac and the viscera exposed. The arm crown is badly damaged and the eyes are lost. The oral face of the web, after preservation for five years in formalin, is a deep sepia, almost black but, when freshly captured, it was velvet black. The mantle length is approximately 60 mm. in the preserved specimen, and this will be used for calculation of the indices noted below. However, when freshly captured, it was slightly larger, ca. 63 mm. The gladius length, measured *in situ,* is ca. 55 mm., which gives an estimated mantle length of 59.8 mm., in good agreement with the actual measurement. The gladius length of the largest male hitherto captured (Specimen 13; PICKFORD, 1948) was only 52 mm. and its mantle length only 55 mm. Evidently the newly captured male is larger than any that have been described previously.

Only the muscular axis of the fins remain and the length measurements may therefore be somewhat too short; the left anterior fin measures 22 mm., the right 26 mm. The latter yields a fin-length index of 36.7 which is lower than the hitherto recorded range for Stage 5 males. However, there is no difference between the sexes in respect to relative fin length, and some Stage 5 females have an index as low as

33. The rostral length of the lower jaw is 8 mm., yielding a rostral-length index of 13.4, which is slightly greater than the highest index hitherto recorded for Stage 5 males, but well below the mean for Stage 5 females. The rostral notch measures 3 mm. and the rostral-notch index of 37.5 is normal.

The condition of the specimen does not permit further description. The condition of the male sex organs suggests that it was probably mature, although spermatophores are not preserved.

Specimens 111 and 112

Two very damaged specimens were taken at Stn 318 in the Bay of Bengal, both were found entangled in the net. Specimen 111 is in slightly better condition than Specimen 112. The visceral mass is badly damaged, the left eye is gone and the right eye enucleated. When freshly captured, the oral face of the web was black. The mantle length could not be measured directly but was estimated from the funnel length and from the rostral length of the lower jaw. The former measures 18.5 mm. and gives a calculated mantle length of 50 mm.; the latter measures 6 mm. and gives a calculated mantle length of 48 mm. The rostral notch measures 2.5 mm. and gives a normal rostral-notch index of 41.7. The specimen appears to be an adult male.

Specimen 112 consists of the buccal mass with fragments of arms, brain and enucleated right eye. There are remains of viscera and fins. The sex is uncertain, but it may have been a female since no male organs could be discovered. The anterior fin length of 27 mm. yields an estimated mantle length of 50 mm. The rostral length of the lower jaw is 6.5 mm., giving an estimated mantle length of 52 mm. The rostral notch is 3 mm., giving a normal rostral-notch index of 46.2.

Specimen 113

One very damaged larva was taken at Stn 471 in the Sunda Trench. The oral face of the web, after five years preservation in formalin, is light brown. The mantle appears to be stretched and the mantle length of 17.5 mm. may be too large. The head width is ca. 10 mm. Both eyes are badly damaged; the eye diameter of ca. 3.0 mm. gives a calculated mantle length of only 12.7 mm. Both anterior and posterior fins are present; they are very damaged on the left side but approximate measurements could be made on the right: right anterior fin length 5 mm., right posterior fin length 4 mm. This larva is obviously in the four-finned Stage 3. The arm crown is in poor condition, but the number of pairs or primary cirri could be counted on some of the arms: there are 7 pairs on the first left, and first, second and third right arms, but possibly only 6 on the third left. The rostrum of the lower jaw measures 2.1 mm., which gives a calculated mantle length of 17.6 mm.; this tends to support the correctness of the actual measurement and casts doubt on the smaller value derived from the diameter of the damaged eyes. The sex is uncertain.

Specimens 114-117

Three metamorphosing larvae, and the eye of a fourth specimen, were taken at Stn. 472 in the Sunda Trench. Some color notes were made on these specimens by Dr. Torben Wolff, at the time of capture. "Specimens A and B (apparently 114 and 115): mouth area sooty black. Ring around the mouth opening and beak has the color given as No. 688 in Séguy (*i.e.* dull violet). Soft parts inside beak the same color. Eyes No. 103 (*i.e.* red), intestine proper (a sketch made at the time suggests that the stomach was intended, G.E.P.) No. 56 (*i.e.* deep red). Specimen C, the one with the arms folded (apparently Specimen 116): mouth area No. 110 (*i.e.* pinkish brown)."

Specimen 114 is very damaged and the right eye is lost, although the optic ganglion remains. The mantle has been pulled away from the exposed visceral mass. The oral face of the web was originally black, as shown by notes on the living specimen cited above, but after five years preservation in formalin it has faded to a light brown. The sex is uncertain, probably female since no penis rudiment could be found. The mantle length, measured from the mid point of the head to the exposed end of the hepatopancreas, is 21 mm., but this is undoubtedly too short and estimates of correct values are given below. The head width, obtained by doubling the distance from the mid point to the outer edge of the left eye lens, is 22 mm. The right anterior fin is contracted and the surface rubbed, it measures only 5 mm., but the left anterior fin, which is apparently attenuated, measures 10.5 mm. The right posterior fin is not preserved but on the left side there is a small rudiment that is badly rubbed. This indicates that the specimen is in Stage 4. The remaining left eye is distorted, but appears to have been about 2.8 mm. in diameter. The arms and web are poorly preserved and no suckers remain. The funnel is well preserved and measures 9 mm.; this gives a calculated true mantle length of 25.1 mm. The rostrum of the lower jaw measures 2.9 mm. and gives a calculated mantle length of 23.9 mm., in good agreement with that derived from funnel length. A mantle length of 24-25 mm. is in the expected range for Stage 4 larvae.

Specimen 115 is a badly rubbed, damaged and distorted larva. Both eyes are present, extruded. As in the previous specimen, the oral face of the web was originally black but has faced to red brown after long preservation. The apparent mantle length of 28.5 mm. may be too long as the specimen is stretched. The head width is 12 mm. Both anterior and posterior fins are present; the left anterior measures at least 6 mm., the right about 5 mm., but the surface is in poor condition. The left posterior fin, which is evidently in the last stages of resorption, measures 1.5 mm. Clearly this is a Stage 4 larva. The arm crown is severely damaged and could not be studied. The left eye measures 6 mm. in diameter, the right 5 mm.; both lenses are damaged. The funnel is 5.5 mm. in length. The rostrum of the lower jaw measures 2.9 mm. The true mantle length may be estimated from each of three measurements and all support the hypothesis that the apparent mantle length is too great: the eye diameter gives a calculated mantle length of 20.6 mm., the anterior fin length ca. 20 mm. and the rostrum 23.9 mm. The sex is uncertain, presumably female.

Specimen 116 was preserved with an everted mantle which protected the fins from undue rubbing. Both eyes remain but the lenses are gone. The arm crown is badly damaged and, as in the two previous specimens, the oral face of the web has faded to a red brown color after long preservation. The mantle length is 17 mm., but this is probably too short. The right eye is 6.2 mm. in diameter and this gives a calculated mantle length of 21 mm. Similarly, the rostrum of the lower jaw measures. 2.9 mm and corresponds to a mantle length of 23.9 mm. The left anterior fin is moderately well preserved and measures 9 mm. in length; the left posterior fin is 3.8 mm. The fins of the right side are badly rubbed. It would appear from the relative lengths of the anterior and posterior fins that the specimen had already passed beyond Stage 3 and was entering Stage 4. The fin light organs and the left composite light organ are preserved. There are six pairs of primary cirri on the left and right fourth arms, and the fourth right arm has a complete set of 7 suckers. This would correspond to a mantle length of about 20 mm. The sex is uncertain, presumably female.

Specimen 117 is represented by an eye with the optic ganglion attached. It cannot be the missing right eye of Specimen 114, taken in the same haul, because the optic ganglion of the latter remains in the head. The eye diameter is 8 mm. and corresponds to a mantle length of 25 mm.; the lens diameter is 3.2 mm. Presumably this specimen was a Stage 4 larva.

Specimen 118

This specimen, from the Tasman Sea, is exceptionally interesting since it represents the southernmost record for the species. It is a moderately well preserved Stage 5 immature female. The skin is badly rubbed on the external surface of the mantle. The oral face of the web is red brown after five years preservation in formalin. The entire web is rotated dorsally over the back of the head, as in JOUBIN's supposed genus "*Retroteuthis*", but this is undoubtedly an accident of preservation. The measurement of mantle length is difficult on account of the abnormal position of the arm crown which conceals the dorsal surface of the head. However, an approximate measurement made from the ventral aspect indicates a length of 31.5 mm. The mantle width is 25 mm., yielding a normal mantle-width index of 79.5. The head width measures 31 mm., giving a normal head-width index of 98.5. Both fins are moderately well preserved but unequally contracted; the left anterior fin measures 13.5 mm. in length, the right 17.0 mm. The fin-length index, based on the longer right fin, is 56.8, which is normal. The fin light organs are preserved in a fold of skin and measure ca. 1.8 mm.: this gives an index of 5.8, in agreement with the expected value.

The arms are somewhat rubbed and damaged, but the number of suckers and primary cirrus pairs could be counted, as follows:

Arm	Number of pairs of primary cirri	Number of suckers
L 1	7	4 + ?
L 2	6 (?)	4 + ?
L 3	5 (?)	6 + ?
L 4	5	9
R 1	7	5
R 2	6	6
R 3	5	3 + ?
R 4	6	9

The maximum and minimum number of primary cirrus pairs is low, in agreement with other speci-

Table 3. Minimum and maximum numbers of pairs of primary cirri on the arms of each specimen of *Vampyroteuthis infernalis* that is sufficiently well preserved to permit study.[1]

Group	Number of specimens with:									
	Maximum number					Minimum number				
	6	7	8	9	10	4	5	6	7	8
Atlantic (previous records)	–	15	20	9	2	1	13	31	7	1
Indo-Pacific:										
Previous records	1	15	10	–	–	4	18	6	1	–
Galathea	–	3	1	–	–	–	1	4	–	–
Total	1	18	11	–	–	4	19	10	1	–

[1] The maximum number is usually on the first or second arms, the minimum number of the third or fourth. Previous data from PICKFORD (1948, 1952).

mens from the Indo-Pacific (Table 3). The maximum number of suckers, 9, corresponds to a mantle length of only 25.5 mm., which is considerably less than the actual measurement. However, previous data showed wide variations which may be attributed, in part, to the fact that new suckers are added intermittently. The smallest number of suckers, 5, is in correct relation to the largest number. The diameter of the largest sucker is 0.9 mm., giving a normal sucker-diameter index of 2.85.

The funnel is stretched and unusually long, measuring 15 mm. which gives a funnel-length index of 47.6, at the upper limit of the range. The eyes are damaged and distorted, the diameter of the left eye is ca. 10 mm., giving an eye-diameter index of 31.8, which is within the normal range but low. The gills are badly rubbed and could not be studied. The rostrum of the lower jaw measures 4.1 mm., giving a rostral-length index of 13 which is slightly below the mean for Stage 5 females and at the upper limit of the range for Stage 5 males. The rostral notch measures 1.9 mm. with an index of 46.3 which is at the upper limit for Stage 5 females.

The foregoing description suffices to show that this specimen is in no way different from other members of its sex and age group, and that it is a fairly typical member of the Indo-Pacific vampyromorph population.

Specimen 119

This is a rather well preserved immature Stage 5 female from the Kermadec Trench. The following color notes were made by Dr. Torben Wolff at the time of capture: "Fin light organ turquoise opalescent with yellowish-green tinge. Gills pale orange. Rectum with white end, otherwise pigmented black. Liver on each side of rectum SÉGUY No. 127 (*i.e.* red brown). Web velvet black. Mouth area as in specimens A and B from Stn 472."

The epidermis is largely rubbed away from the external surface, except on the oral face of the web which is red brown after five years in neutral formalin. Dr. WOLFF injected the vascular system with a carmine suspension, but unfortunately the carmine has dissolved in the preserving fluid (presumably owing to its alkalinity) and the entire specimen is now stained deep purple. The eyes are sunk in the gelatinous tissues of the head. The dorsal sectors of the web are rotated backwards in the manner of JOUBIN's supposed vampyromorph genus "*Retroteuthis*", but this is undoubtedly the result of abnormal contraction of the dorsal musculature. The mantle measures 41 mm. in length; the mantle width is 29 mm. giving a mantle-width index of 70.7 which is normal for Stage 5 females. The head width is 30 mm., which gives a head-width index of only 73, this is unusually low for Stage 5 specimens of either sex. The left anterior fin measures 18.5 mm. in length, the right only 16 mm.; the fin-length index, based on the longer left fin, is 45.1, which is in the normal range for Stage 5 specimens of either sex. Fin light organs are present, rubbed up in folds of skin. The right composite light organ is also preserved; it has a length of 2.3 mm. giving an index of 5.6, which is normal. The number of luminescent nodules is ca. 70, which is in the high range but not unusual.

The arms are moderately well preserved and the number of suckers and primary cirrus pairs could be counted in most instances, as follows:

Arm	Number of pairs primary cirri	Number of suckers
L 1	7	10
L 2	8	9 or 10
L 3	7	9 + ?
L 4	7	13
R 1	–	–
R 2	7	10 or 11
R 3	8	12
R 4	6	13

The maximum number of cirrus pairs, 8, is at the upper limit for the Indo-Pacific (Table 3). The maximum number of suckers, 13, occurs, as expected, on the ventral arms and corresponds to that calculated for a specimen measuring 37 mm. in mantle length. This is in reasonable agreement with the actual measurement. The minimum number of 9 or 10 is also in agreement with the predicted value.

The rostrum of the lower jaw measures 5.0 mm. and the rostrallength index of 12.2 is at the lowest limit for Stage 5 females. The rostral notch measures 2.0 mm. and gives an index of 40, which is typical.

DISCUSSION

A. *Morphological Characters*

In the preceding descriptions of the specimens constant reference has been made to expected indices, and other calculated standards of reference, derived from a previous study of the Dana collections (Pickford, 1948). Measurements and indices were compared with their expected numerical values and, when appreciable differences were noted, attention has been called to this circumstance. However, in no instance, were the deviations of sufficient magnitude to warrant a change in the basic assumption that there is but a single species of *Vampyroteuthis*, widely distributed in the middle depths of all tropical and subtropical oceans.

Special attention has been directed towards the following three problems: the natural color of the species, the problem of differences of size and bodily proportions between adult (Stage 5) males and females, and the possibility of racial differences between the Indo-Pacific and Atlantic Oceans.

It was observed by the zoologists of the Discovery Expeditions (Pickford, 1952) that freshly captured specimens were deep purple in color, not black as formerly supposed. Moreover, the oral face of the web was black, not red brown as previously described. Some of the specimens captured by the Galathea in the Bay of Bengal were studied by the present author at the time of capture. Unfortunately they were all extremely damaged and most of the skin was rubbed away from the outer surface of the body. Presumably owing to this circumstance, none of these specimens showed the purple color described by the Discovery Expedition, but in all instances the oral face of the web was black. The oral face of the web was also black in the large female from Stn. 190 (Specimen 105), examined two months after preservation in neutral sea water formalin, and in the damaged specimen from Stn 279 (Specimen 107) which was preserved in alcohol and examined two weeks after capture. All the remaining specimens, examined five years after preservation in formalin, have a more or less faded, sepia or red brown web. But color notes on some of these specimens, made by Dr. Torben Wolff at the time of capture, indicate that here also the oral face of the web was originally a sooty black.

Apart from primary and secondary sexual characters, the following suspected differences between adult males and females were noted previously: males are smaller at sexual maturity, the mantle width is narrower, the shortest arms may be relatively shorter, the composite light organ is apparently smaller, the lower jaw is significantly smaller and the length of the rostral notch slightly greater; it is also possible that the gladius length is slightly shorter in relation to mantle length. As far as the data permit, attention has been paid to each of these characters, as follows:

1. The range for absolute mantle length in sexually mature specimens is extended upwards for both sexes by the Galathea material, but the sex difference remains. Female Specimen 105 measures 100 mm., as compared with 65 mm. and an estimated 76 mm. for the two previously described females. The male form the same station (Specimen 106) measures 46 mm. and is in the range covered by four previously described mature males (44-55 mm.), but a male from the Bay of Bengal (Specimen 110), which was presumably mature, measures 60 mm.

2. In respect to mantle width, the new data for Stage 5 specimens (3 females and one male) has no significant effect on the mean mantle-width index, although the largest female is unusually narrow, perhaps because it had recently spawned. The revised mean mantle-width index for 14 Stage 5 females is now 74, instead of 75; the revised mean for 11 males is 65, instead of 64.

3. The arm crown was not sufficiently well preserved in any of the specimens to permit study of relative arm length.

4. The composite light organ is preserved in only two Stage 5 specimens (Specimens 105 and 119). Specimen 105 has an unusually small composite light organ for a female, but the other is normal. The revised range and mean for the composite light organ-length index of Stage 5 females (11 specimens) is 4.2-*6.4*-9.1, as compared with a previous range and mean of 5.1-*6.7*-9.1. The revised mean is still well above the mean for Stage 5 males, and the ranges do not quite overlap, 4.0-*4.7*-6.4. It still seems probable that the composite light-organ

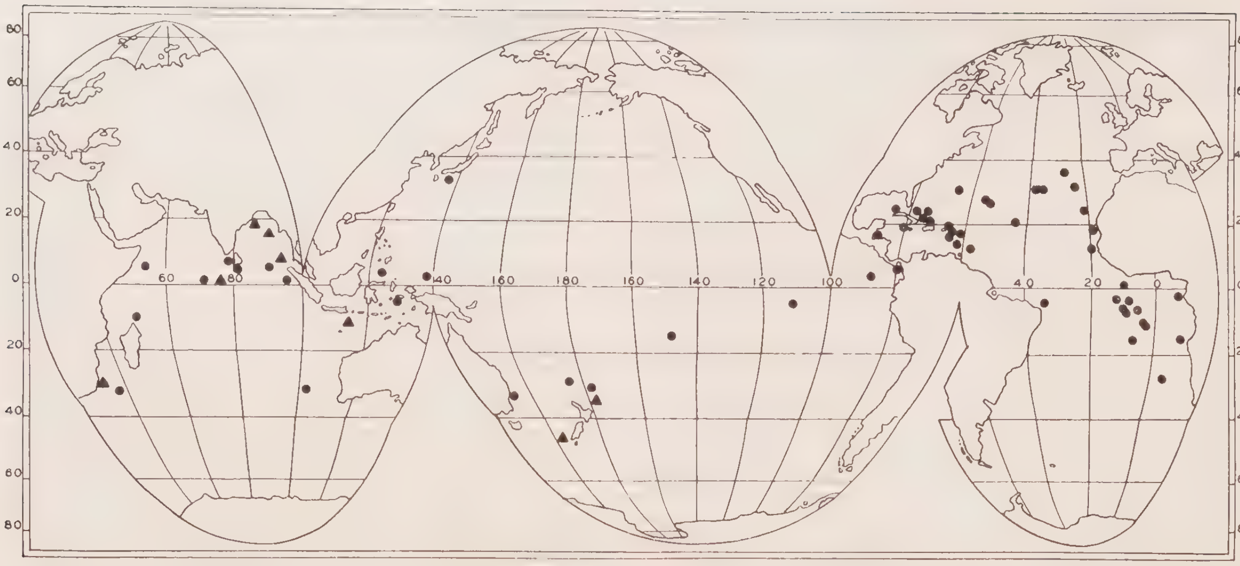

Figure 1. *Vampyroteuthis infernalis* Chun. Distribution. ● Previous records. ▲ New records by the Galathea Expedition.

may be relatively larger in adult females, despite the new low recorded for Specimen 105.

5. The new data (3 females and 2 males) tends to confirm the hypothesis that females have relatively larger jaws, although one female (Specimen 119) had an unusually small rostral-length index for specimens of this sex. The revised mean rostral-length index for 15 females is essentially the same as before, 14.4; the revised mean for 11 males is unchanged, 11.9. There seems to be little doubt that there is a sex difference in respect to this character.

6. On the other hand, data for the length of the rostral notch (3 females and 3 males) fails to clarify the supposed sexual difference. The mean for 12 females is reduced from 41 to 40, and the mean for 12 males is reduced from 45 to 44. The change is insignificant.

7. The relatively long gladius of the sexually mature female (Specimen 105) tends to confirm the possibility that this structure may have a somewhat greater relative length in females.

The only real difference between Atlantic and Indo-Pacific specimens concerns one character, the number of pairs of primary cirri on the arms. A study of the fine series in the Dana collections indicated that Atlantic specimens tended to have one more pair of primary cirri than those from the Indo-Pacific. This hypothesis was supported by an examination of the Discovery specimens (PICKFORD, 1952). Not many of the Galathea specimens have an arm crown that is sufficiently well preserved to determine this character, but as far as the evidence goes (Table 3) the results appear to confirm the previous findings. There are no exceptions to the rule that Indo-Pacific specimens never have more than a maximum of 8 pairs (usually on the first or second arms) and more than a minimum of 7 pairs (usually on the third or fourth arms). The typical maximum number for the Indo-Pacific is 7, the typical minimum number 5, whereas in the Atlantic the typical maximum number is 8 and the typical minimum number 6.

B. *Distribution and Biology*

Some of the new records add valuable information regarding the geographical distribution of the species (Fig. 1). The two specimens from off Durban (Specimens 105 and 106) are of special interest because there has been only one previous record, taken by the Discovery Expedition, from this region. The newly established records from the Bay of Bengal and the Sunda Trench confirm the wide occurrence of *Vampyroteuthis* in the Indian Ocean. There are still no records from the South China Sea, although one of the pelagic hauls was made in this area at a depth of 3400-3800 m. in the express hopes of catching *Vampyroteuthis* (Stn. 407). The depth may have been too great, however. Two of the Dana specimens were taken in the East Australian Basin, but the new record from the Tasman Sea (Specimen 118) is considerably further south. It is, in fact, the southernmost record for the species. The Dana Expedition collected specimens from north of New Zealand and the new record from the Kermadec Trench (Specimen 119) establishes the widespread occurrence of *Vampyroteuthis* in this general area.

Two hypotheses advanced previously (Pickford, 1946) appear to receive partial support from our enlarged knowledge of the distribution of *Vampyroteuthis*, *viz.* 1. that the species can pass from the Atlantic to the Indian Ocean by way of South Africa, and 2. that it can pass from the Indian to the Pacific Ocean not only by way of the East Indies but also south of Australia. However, no specimens have yet been taken either from the region directly south of Cape Agulhas or from the waters south of Australia, so that final proof is still lacking.

Most of the Galathea specimens were caught in bottom hauls from deep water but, since open nets were employed, there is no evidence that they could not have entered the nets during lowering or raising. The data on depth distribution therefore provides no decisive evidence that would extend our knowledge of the vertical distribution of the species to greater depths than those hitherto recorded. In a few instances, where hauls were made in middle depths, the range is in agreement with previous records which indicate that this bathypelagic species occurs most abundantly between 1500 and 2500 m. and that none have been taken in depths of less than 300 m.

Two sexually mature specimens, a male and a female, were taken together in the same haul, off Durban in February, 1951 (Specimens 105 and 106). A very large adult male (Specimen 110) was taken in the Bay of Bengal in April, 1951; it was probably sexually mature although the poor state of preservation did not permit observations regarding the presence of ripe spermatophores in the ducts. An attempt was made previously (Pickford, 1946) to determine whether there was a seasonal difference in the frequencies of capture of young larvae or sexually mature adults that would throw light on the possible occurrence of a breeding cycle. The results were indecisive on account of the geographical scattering of the stations, the small numbers taken at the same time in any one locality, and the fact that no one area has been collected at all seasons of the year. However, larvae appear to occur at all times of year and the evidence regarding sexual maturity was fragmentary. The best data was for the Indo-Australian Basin in which there were indications that sexually mature individuals were absent from the catches in September and October and appeared in November and December. Even if this could be established, which is doubtful, the breeding period must be different in other regions. A single mature female was taken by the Princess Alice in the Monaco Deep in August, and a mature male and female were captured by the Dana Expedition in January and September respectively, in the Gulf of Panama. The new records tend support the view that sexually mature individuals may be found at all seasons of the year, but if the breeding season in the Indian Ocean begins in November the capture of a spawned out female in February (Specimen 105) would be expected.

SUMMARY

Fifteen specimens of *Vampyroteuthis infernalis* Chun were captured by the Danish Deep-Sea Expedition in the Indian Ocean and Western Pacific, making a total of 120 known specimens. Measurements and indices confirm the hypothesis that there is only a single species, but the number of pairs of primary cirri is less in the Indo-Pacific than in the Atlantic Ocean confirming the hypothesis that there may be a racial difference between these regions. The oral face of the web is black in freshly captured specimens, confirming the observations of the Discovery Expedition, but the color fades to brown after long preservation in formalin. A sexually mature male and female were taken off Durban, South Africa; the female, which had recently spawned, is 25 % larger than any hitherto captured but does not differ significantly in its proportions. An adult male from the Bay of Bengal is somewhat larger than any hitherto recorded for this sex. New data confirms the hypothesis that adult females are larger than adult males, and that there are minor sex differences in the bodily proportions of Stage 5 males and females.

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THE WHALE-FISHES:

FAMILIES CETOMIMIDAE, BARBOURISIIDAE AND RONDELETIIDAE (ORDER CETUNCULI)

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INTRODUCTION

The "Galathea" Deep-Sea Expedition Round the World 1950-1952 collected in the Indian Ocean noteworthy examples of the rare "whale-fishes", an order of primitive bony fishes of which less than 50 specimens have been previously recorded.

The "Galathea" Expedition obtained six specimens, representing all three known families of the order Cetunculi, including the Barbourisiidae which was known only from the unique type. Also included are two new species of the genera *Gyrinomimus* and *Cetomimus* of the family Cetomimidae.

The method of investigation followed in this report is that of Harry (1952), whose paper summarized the literature to date on the whale-fishes. Subsequent to that paper Koefoed (1955) and Rass (1955) have recorded additional material and added new species in the family Cetomimidae.

The author wishes to express his gratitude to Dr. Anton F. Bruun, leader of the "Galathea" Expedition, for allowing him to examine and report upon these remarkable fishes, and to the George Vanderbilt Foundation at Stanford University for its support of the studies. The illustrations are by Mrs. Janet (Roemhild) Canning, scientific illustrator of the George Vanderbilt Foundation. The fishes are of the collections of the Universitetets Zoologiske Museum, Copenhagen.

FAMILY CETOMIMIDAE

Cetomimus indagator n. sp.

(Fig. 1, pl. 1)

Holotype: 120.2 mm. in standard length; from off the east coast of South Africa, 32°33'S. Lat., 32°01'E. Long., "Galathea"-Expedition 1950-52 station 186; 31 Jan. 1951, time 1645. Bottom Globigerina ooze. Depth 3620 meters; 7000 meters wire out.

Description of Galathea type: The only known specimen is in moderately good condition except that the skin is lacerated in many places and the lateral-line is greatly torn; however, the tips of the fin rays are all present and all characters utilized in cetomimid descriptions are present, except for parts of the lateral-line.

Body oval in cross-section behind head. Greatest depth at nape. Caudal peduncle much longer than deep. Anus well before anal fin by a distance equal to pectoral fin length. No distinct cavernous luminous tissue present on head, body or fins (see discussion of glandular tissue about anal fin origin under section on that fin).

Head very large, strongly compressed; head width slightly greater than body width, approximately 1.5 in head depth. Profile of snout to nape rounded at snout and relatively straight posteriorly. Nostrils similar to head pores, close together on each side, situated approximately an eye diameter above the upper jaw. Nasal organ a thin straight membrane, more prominently developed in anterior nostril, slightly ridged, without development of olfactory laminae. A line between tip of snout and eye touches lower border of anterior nostril. Eyes small, slightly nearer upper jaw than profile of head. Interorbital very broad, strongly convex, with one lateral projection forward on each side.

Mouth enormous, moderately oblique. Dentigerous margins of jaws slightly concave. Rictus approximately two eye diameters before posterior tip of premaxillary. Posterior end of jaws well before edge of gill cover. Mandible without lateral processes. Tip of angular rounded, without spines. Distance between ricti 2.5 into upper jaw length. Teeth on jaws granular, in many irregular series on both jaws. The individual teeth are tiny, always pointed, and either conical or incisiform. Dentition on jaws as in text-fig. 1A and B of Harry (1952, p.

60). Teeth on lower jaw extend posteriorly to rictus, but not beyond. Teeth on vomer and palatines similar in shape to those on jaws, depressible. Vomer very small, diamond-shaped, with about four rows of teeth, seven in longest central row. A single small slender palatine bone situated laterally under eye; palatine with two longitudinal rows of teeth, 15 teeth in longest (inner) row. Copula on tongue small, long and slender, club-shaped, posterior end largest, rounded; anterior end pointed. Length of copula about 2.2 in snout length; narrowest width of copula about one-tenth its length. Teeth on copula similar to those in jaws, covering entire bone, without separate rows of teeth; approximately 30 irregular rows of depressible teeth along its length.

Four gill arches present, a slit present behind last arch. Holobranchs very poorly developed, shorter in length than width of gill arches. Normal gill rakers absent; their function performed by small round bony plates covered with gill-teeth which are minute, granular, fixed, similar to dentition in jaws. Each gill-plate with approximately 15-40 teeth. First gill arch with 3+10 round dentigerous plates, of which 3 plates are on the hypobranchial. Pharyngobranchial teeth in two small, oval, high-crowned patches of tiny depressible teeth. Anterior pharyngobranchial teeth in five rows, approximately seven teeth in longest rows. Posterior pharyngobranchial teeth in four rows, approximately 10 teeth in longest row.

Lateral-line a broad tube, pierced by 12 pores on body from upper posterior edge of gill opening to base of caudal fin. Original structure of pores, tubes and flaps on lateral-line not preserved. Apparently the pores along the lateral-line are all large, with no flaps or only small flaps. Numerous large pores on head.

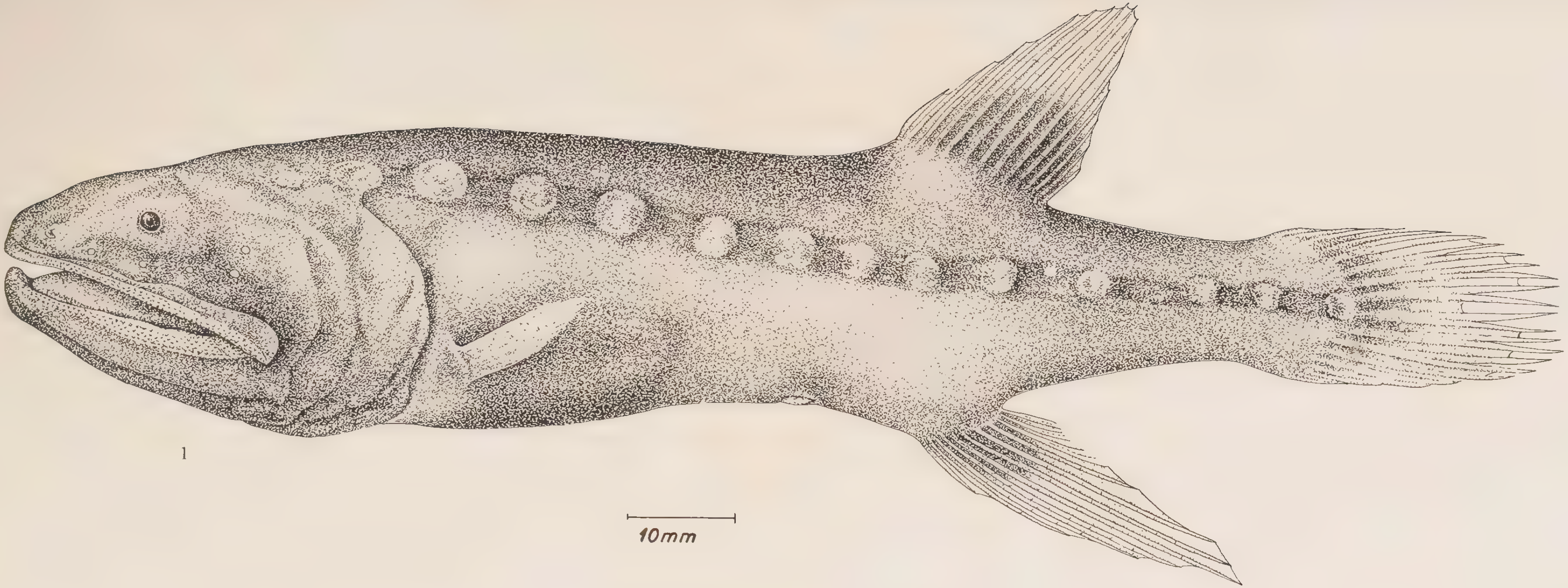
Skin delicate, smooth, lacking scales and spicules, but not loose and flabby.

Dorsal and anal fins far back on body. Dorsal fin origin in advance of a vertical from anal fin origin, but behind anus. Dorsal fin with 14 rays, all simple. Anal fin with 13 rays, all simple. In both the dorsal and anal fins the last two rays are split to the base and counted seperately. The anal fin has a superficial appearance in profile of being abnormally constricted at the base, but it is completely normal, providing this species with a unique form in this fin. The anal fin of this species is also unique in the whale-fishes in the form of its luminous organ. About the base of the anterior rays are small hollow streaks along the surface that appear to correspond to the cavernous tissue in more advanced species. These streaks are connected to a reticulate pattern of minute granule-filled canals over the surrounding region. Pectoral fin situated low, somewhat more elongate than usually found in cetomimids, middle rays prolonged. Pectoral rays 18 on each side. Pelvic fins absent. Caudal fin large, slightly emarginate. Principal caudal fin rays 5+6.

Coloration: Uniformly solid dark brown in alcohol. Tips of fins light. Interior of mouth almost completely unpigmented. Inside of operculum lightly pigmented.

Measurements in percent of standard length: Body depth measured at a vertical from region of pectoral fins 22.9. Caudal peduncle length, which is the oblique distance between the end of the anal base and mid-base of caudal fin 24.5. Least depth of caudal peduncle 08.5. Head length measured from the anterior tip of the snout (upper jaw) to the most distant point on the opercular margin including membranous flaps, 32. 9. Snouth length measured from the anterior tip of the snout (upper jaw) to the anterior margin of the fleshy orbit 11.5. Upper jaw length, which is the distance between the tip of the snout and posteriormost point of the premaxillary 22.8. Eye diameter, which is the greatest visible distance, without dissection, across the orbit, and corresponding to the diameter of the opaque cornea 01.5. Interorbital width, which is the least fleshy width 13.1. Greatest head width measured between the sides of the premaxillaries 15.6. Distance between tip of snout and visible base without dissection of first dorsal fin ray 69.7. Dorsal fin base length from origin of first ray to base of last ray 11.8. Distance between tip of snout and anus 61.6. Length of anal fin base from origin of first ray to base of last ray 71.6. Length of pectoral fin measured from base of longest middle ray to its tip 08.7. Length of caudal fin from mid-base (measured from the fold when the fin is flexed from side to side) to a vertical from tip of longest ray 19.0.

Relationships: The species *indagator* clearly belongs in the genus *Cetomimus,* agreeing with the characters used by Harry (1952), Parr and others to distinguish this genus. It reveals in general form closest affinities to *Cetomimus kerdops* Parr in the previously monotypic subgenus *Psapharocetus* and keys out to this group in Harry's key (1952, pp. 59-60). Therefore, this new species further sub-



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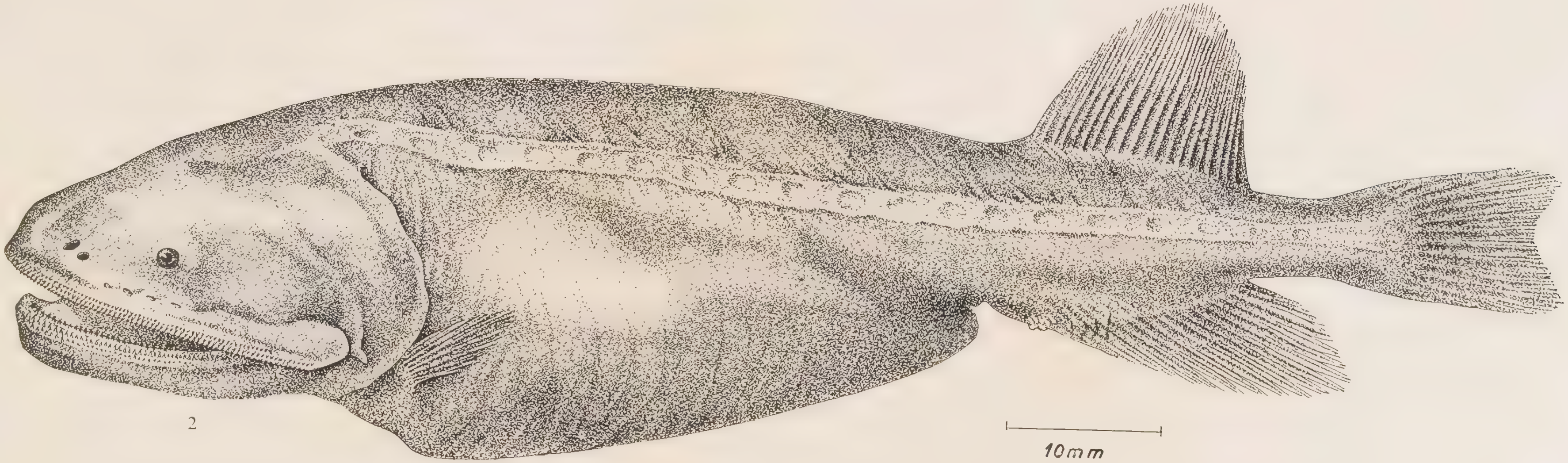

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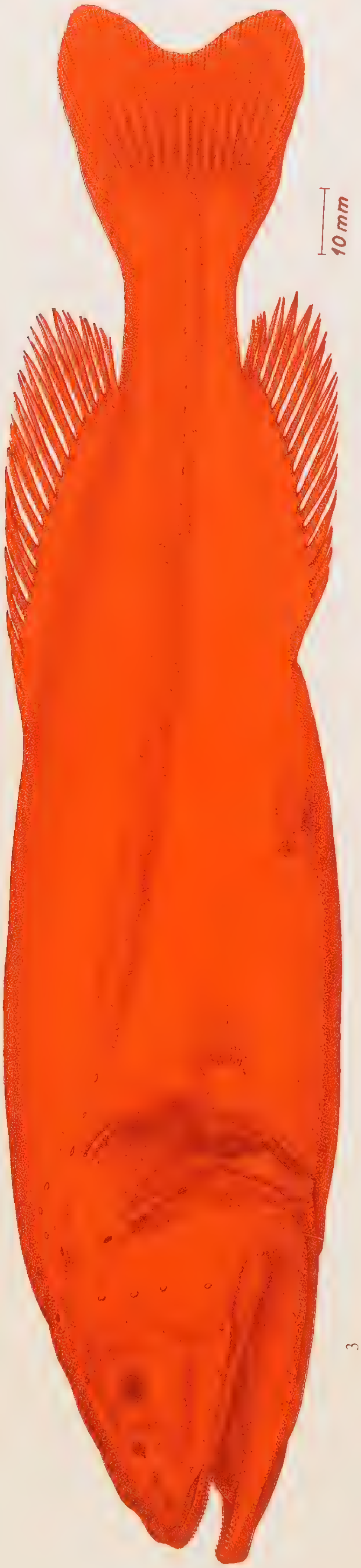
Fig. 1. Holotype of *Cetomimus indagator*, new species, from station 186 of the "Galathea"-Expedition 1950-1952 off the east coast of South Africa.
Fig. 2. Holotype of *Gyrinomimus bruuni*, new species, from station 234 of the "Galathea"-Expedition 1950-1952 from off Kenya.



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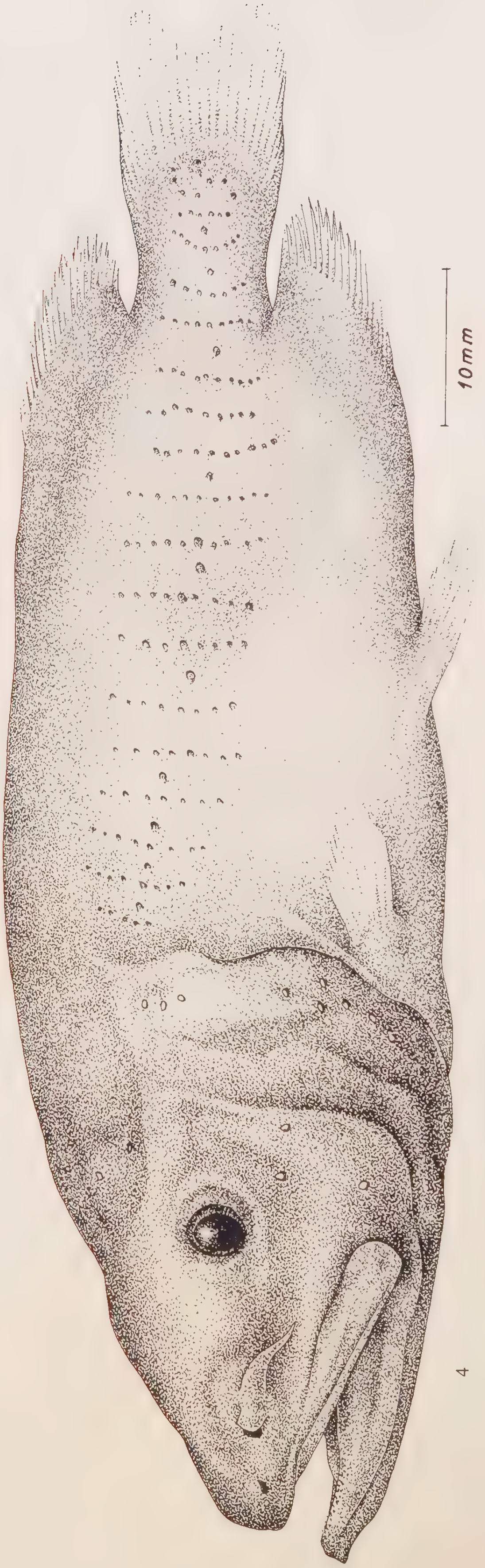

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Fig. 3. *Barbourisia rufa* Parr. Second known specimen 211 mm. in standard length from station 220 of the "Galathea"-Expedition 1950-1952 from off Madagascar.
Fig. 4. *Rondeletia bicolor* Goode and Bean. Specimen 84.8 mm. in standard length from station 466 of the "Galathea"-Expedition 1950-1952 from the Sunda Trench.

stantiates *Psapharocetus* as a valid subgenus of *Cetomimus*, which now should include both *kerdops* and *indagator*. The new species is similar to *kerdops* in narrow, moderately pointed head (when viewed dorsally), separating it sharply from all other species of *Cetomimus*, which all have broad heads and wide-spread jaws.

Cetomimus indagator trenchantly differs from *kerdops* in number of lateral-line pores (12 versus 25), anal fin rays (13 versus 17) and angular spines (absent versus large spine-like lateral protuberances present).

Cetomimus indagator differs markedly from the recently described *Cetomimoides parri* Koefoed in dorsal fin rays (14 versus 26), anal fin rays (13 versus 20) and in most body and fin proportions.

Cetomimus indagator differs grossly from the recently described *Vitiaziella cubiceps* Rass in head, body and fin proportions, size of mouth (extending far behind eye versus terminating before a vertical from eye), and pectoral fin rays (18 versus 9).

Name: *indagator* (Latin) means explorer.

Gyrinomimus bruuni, n. sp.

(Fig. 2, pl. 1)

Holotype: 86.7 mm. in standard length; from off Kenya, 5°25′S. Lat., 47°09′E. Long., "Galathea"-Expedition 1950-52 station 234; 10. March 1951, time 1705. Bottom Globigerina. Depth 4820 meters; 7400 meters wire out.

Description of Galathea type: The only known specimen is in good condition except the tips of the vertical fins' rays are broken off. These rays have been reconstructed in the illustration (fig. 2) after the condition in other species of *Gyrinomimus*.

Body teardrop-shaped in cross section behind head, ridge of back sharp-edged. Belly distended with food. Greatest depth in region of pectoral fins. Caudal peduncle distinctly longer than deep. Anus immediately before anal fin; cavernous luminous tissue present on each side of anus in the form of short oblique streaks.

Head large, compressed; head width slightly less than greatest head depth. Profile of snout to nape moderately rugose in preserved specimen but probably rounded in life as in illustration. Nostrils not easily distinguished; appearing exactly the same as large head pores. Nostrils close together on each side and close to upper jaw. Anterior nostril round, its diameter appreciably less than eye diameter, its anterior margin rimmed by a forward projecting lappet, which is adnate to surface of snout; at first glance this lappet appears to be a reclining raised rim. Posterior nostril round, approximately 2-3 times larger in diameter than anterior nostril, separated from anterior nostril by a very narrow membrane less in width than diameter of anterior nostril. Nasal organ a thin straight membrane, more prominently developed in anterior nostril, slightly ridged, without development of olfactory laminae. A line between eye and tip of snout touches lower border of anterior nostril; posterior nostril above line. Eyes small, nearer upper jaw than profile of head. Interorbital very broad, strongly convex, with two lateral projections; median region slightly concave.

Mouth enormous, moderately oblique. Dentigerous margin of upper jaw slightly sigmoid in outline; that of lower jaw distinctly curved, concave. Rictus approximately four eye diameters before posterior tip of premaxillary. Jaws extend posteriorly almost to edge of gill cover. Mandible with a short lateral process behind tip of upper jaw and tip of the angular produced into two pointed spines. Distance between ricti 1.7 into upper jaw length. Teeth on jaws arranged in three distinct cardiform rows, as in text-fig. 1C and D of Harry (1952, p. 60); teeth curved, elongate, individual teeth of innermost series longest. Teeth in lower jaw similar to those in upper, with approximately 90 teeth in the middle series along the mandible, extending posteriorly well beyond the gape. Teeth on vomer and palatines similar in shape to those on jaws, depressible. Teeth on vomer arranged in two straight, parallel, transverse rows; anterior row with eight, posterior row with 10 recurved incisors. Palatine series divided into two patches on each side. The teeth on the anterior section are arranged in three crescentic series; there are about 18 teeth in the longest row. The posterior tip of the anterior patch is slightly over one eye diameter before a vertical from the eye. Posterior palatine with two rows of teeth in a long narrow patch of two closely applied sections, extending posteriorly to rictus; approximately 70 teeth in longest inner series, including counts for overlapping teeth in inner series. Teeth on copula of tongue in a shield-shaped patch, slightly constricted across middle, outline rounded at posterior end, pointed at anterior end. Length of copular patch about 1.6 in snout length; with 16 irregular rows of depressible teeth along its length; narrowest width of copula about one-third its length. None of copular teeth rows separated from remainder.

Four gill arches present, no slit behind the last. Holobranchs well developed, their length approximately thrice the width of the gill arch. Normal gillrakers absent; their function performed by flat bony plates covered with gill teeth which are minute, granular, fixed, arranged in five series across the plates. Teeth on hypobranchial of first arch on two elongate bony patches with 9-13 teeth each in the longest row. Teeth on ceratobranchial of first arch in a single long patch preceeded by and followed by a tiny patch; approximately 70 teeth in a longitudinal row on long patch. Teeth above angle on epibranchial on first arch in a single long slender patch, with about 30 teeth in a longitudinal row; preceeded by a small circular patch at angle. Pharyngobranchial teeth in two elongate high-crowned patches on each side; individual teeth similar to those on jaws. Anterior pharyngobranchial teeth in three rows; inner row longest, about 18 teeth in length. Posterior pharyngobranchial teeth in four rows, about 24 teeth in longest row.

Lateral-line a broad tube, pierced by 19 pores on body from upper posterior edge of gill opening to base of caudal fin, the last two pores with moderately developed flaps on their anterior margins; flaps shorter than pores; posterior pores small, much narrower than lateral-line tube. Lateral-line membrane between pores generally has one or two median mucus-tubes anteriorly and two mucus-tubes (one above the other) posteriorly. Longitudinal keel on membranes between pores only slightly developed, anteriorly not evident. Scattered mucus-tubes present on the caudal fin behind the last pore. No scattered mucus tubes noticed on back. Numerous large pores and a few mucus-tubes scattered over head.

Skin loose and flabby over head and body; skin smooth, completely lacking scales and spicules. No cavernous luminous tissue present about dorsal fin. Anal luminous tissue primarily associated with anus, as previously described. Otherwise no luminous organs evident. Four small lappets present anteriorly along base of anal fin.

Dorsal and anal fins far back on body. Dorsal fin origin well in advance of a vertical from anal fin and anus. Dorsal fin with 20 rays, at least the first five and last two rays simple. End of dorsal fin base opposite end of anal fin base. Anal fin with 18 rays, at least the first five and last two rays are simple. Both the anal and dorsal fins have the tips of the middle rays broken, and the branched rays cannot be counted; the last two rays are split to the base and counted separately. Pectoral fin short, low, directed obliquely upward, outline evenly rounded; pectoral rays 18 on each side. Pelvic fins absent. Caudal fin short, tips of rays broken off in type.

Coloration: Uniform solid dark brown in alcohol. Tips of fins light. Roof of mouth dark brown to black. Inside of operculum lightly pigmented brown.

Measurements in percent of standard length: Body depth measured at a vertical from region of pectoral fins 27.5. Caudal peduncle length, which is the oblique distance between the end of the anal base and mid-base of caudal fin 10.5. Least depth of caudal peduncle 05.9. Head length measured from the anterior tip of the snout (upper jaw) to the most distant point on the opercular margin including membranous flaps 31.5. Snout length measured from the anterior tip of the snout to the anterior margin of the fleshy orbit 11.9. Upper jaw length, which is the distance between the tip of the snout and posteriormost point of the premaxillary 25.8. Eye diameter, which is the greatest visible distance, without dissection, across the orbit, and corresponding to the diameter of the opaque cornea 01.6. Interorbital width, which is the least fleshy width 14.3. Greatest head width measured between the sides of the premaxillaries 19.6. Distance between tip of snout and visible base without dissection of first dorsal fin ray 74.0. Dorsal fin base length from origin of first ray to base of last ray 17.1. Distance between tip of snout and anus 71.0. Length of anal fin base from origin of first ray to base of last ray 15.5. Length of pectoral fin measured from base of longest middle ray to its tip 09.8.

Relationships: The new species *bruuni* clearly belongs in the genus *Gyrinomimus*, agreeing well with the genus as delimited by Parr (1934, 1946) and Harry (1952). Three specimens of two species of *Gyrinomimus* are known, *G. simplex* Parr and *G. myersi* Parr. All three specimens have been compared to the new species *G. bruuni*.

Bruuni is significantly differentiated from the previous known species of *Gyrinomimus* by gill structure and other characters as shown in the following key. It is most closely related to *G. simplex*, as evidenced by lateral-line form, dentition and general body and head form.

Name: *bruuni* is named after Dr. Anton F. Bruun, leader of the "Galathea" Deep-Sea Expedition Round the World 1950-1952, and foremost investigator of the marine life of the greatest depths.

Key to the species of the genus Gyrinomimus

1a. Four distinct gill arches present, bearing holobranchs. Distinct cavernous luminous tissue present about anal fin origin. 20 dorsal rays. 19 lateral-line pores between gill opening and caudal fin......... *Gyrinomimus bruuni,* n. sp.
1b. Three distinct gill arches present, bearing holobranchs. No distinct cavernous luminous tissue. 17 dorsal rays. 15 lateral-line pores.
2a. Long pointed flaps covering lateral-line pores. Three rows of teeth on vomer.................................. *Gyrinomimus myersi* Parr
2b. Lateral-line pores lacking flaps. Two rows of teeth on vomer.... *Gyrinomimus simplex* Parr

FAMILY BARBOURISIIDAE

Barbourisia rufa Parr
(Fig. 3, pl. 2)

Specimen taken by the "Galathea"-Expedition: One 211 mm. in standard length; from off Cape Amber, Madagascar, 11°43'S. Lat., 49°09'E. Long., "Galathea"-Expedition 1950-52 station 220; 1. March 1951, time 1930. Depth 1070-1360 meters; Triangular pelagic Trawl, 2000 meters wire out. Estimated fishing depth 450-700 meters.

This specimen agrees well in all characters with the holotype of *Barbourisia rufa* Parr as described and figured by Parr (1945). Since the species previously was only known from the holotype, this second specimen of a very rare family is quite important. In the first place it settles an argument about the validity of the family and possible teratological nature of the unique type, see Myers (1946) and Parr (1945, 1946b). Also, the "Galathea" specimen reveals very close similarities to the type, which is interesting because the two specimens were taken in different oceans, the type having been collected in the Gulf of Mexico. It appears likely that the family and species occurs worldwide at mid-depths and over this range has little variability. A comparison of the two specimens known can be made from fig. 3 and pl. 1 of the holotype (Parr, 1945), both of which were drawn by the same illustrator.

Description of "Galathea" specimen: Skin of head and body covered with minute imbedded spines. No luminous organs evident. Jaws covered with tiny granular teeth as in figs. 1A and B of Harry (1952). Vomer very small, oval, with approximately 15 minute teeth. No palatine teeth present. Four gill arches present, a small slit behind last arch. Normal gillrakers present, $4+15$ on first arch.

Dorsal fin rays 22; 11 simple rays followed by 10 branched rays and a simple ray. Anal fin rays 18; 4 simple rays followed by 13 branched rays and a simple ray. Last two rays of dorsal and anal fins separated to base and counted separately. Pectoral fin rays 14. Pelvic fin rays 6. Lateral-line pores 32 between upper posterior margin of head and caudal fin.

Coloration: Externally, head, body and fins completely unpigmented in formalin. Epidermis diaphanous. Inside of mouth unpigmented. Inside of operculum dark brown. When alive the fish was of a beautiful red color with a tint of orange in it.

FAMILY RONDELETIIDAE

Rondeletia bicolor Goode and Bean
(Fig. 4, pl. 2)

Specimens taken by the "Galathea" Expedition: Three specimens 65.4-84.8 mm. in standard length.

65.4 mm. S.L.; from off Ceylon-Calcutta, 17°10' N. Lat., 84°30'E. Long., "Galathea"-Expedition 1950-52 station 299; 24. April 1951, time 1725. Bottom mud. Depth 2820 m.; 5300 meters wire out.

84.7 mm. S.L.; from off Ceylon-Calcutta, 19°30' N. Lat., 86°32'E. Long., "Galathea"-Expedition 1950-52 station 301; 25. April 1951, time 1810. Depth 1110 meters; triangular pelagic trawl, 2100 meters wire out. Estimated fishing depth 700-800 meters.

84.8 mm. S.L.; from the Sunda Trench, 10°21'S. Lat., 11°12'E. Long., "Galathea"-Expedition station 466; 6. Sept. 1951, time 0835-1035. Bottom bluish clay. Depth 7160 meters. 10,600 meters wire out.

The three "Galathea" examples agree closely with the previous accounts of the species, establishing the family outside of the Atlantic Ocean for the first time. This material and other collections to be reported upon elsewhere establishes the family and species as round-the-world in distribution.

Description of "Galathea" specimens: These rondeletiids are in excellent, complete condition. Jaws covered with tiny granular teeth as in text-figs. 1A and B of Harry (1952). Vomer and palatine teeth absent. Four gill arches present with a small slit behind last arch. Normal gillrakers present, 6+14 on first arch.

Dorsal fin rays 14. Anal fin rays 13. Counts for dorsal and anal fins were determined by detailed dissection of the fin bases; the last two rays are separate to the base and counted separately. Pectoral fin rays 9. Pelvic fin rays 5. Principal caudal fin rays 9+10. All the counts have been prepared from the largest example from the Java Deep.

Coloration: Uniformly solid dark brown in alcohol. Tips of fins light. Inside of mouth and operculum lightly pigmented.

CONCLUSIONS

This report on cetunculous fishes collected by the "Galathea" Expedition 1950-52 establishes the first substantial collections of whale-fishes from the Indian Ocean; previously, all but two examples of the order had been recorded from the Atlantic Ocean. Undoubtedly, as this bizarre fish group becomes better known, it will be shown to be circum-orbital in distribution and as abundant in the Pacific and Indian Oceans as in the Atlantic.

Present studies of the Galathea example of *Barbourisia rufa* Parr, the monotypic member of the Barbourisiidae, further confirms the conclusions (Harry, 1952) about the close relationship of this family to the Cetomimidae and Rondeletiidae. The characteristics of *Barbourisia,* such as in dentition, gill arch structure, lateral-line form, and fins, are distinctly intermediate between the Cetomimidae and Rondeletiidae.

The "Galathea" Expedition 1950-52 resulted in the addition of two new species to the whale-fish group, which now totals 13 species recognized in the Cetomimidae, and one each in the Barbourisiidae and Rondeletiidae. Continuing studies clearly indicate that the number of valid species of Cetunculi will be more than doubled before all the forms are known.

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